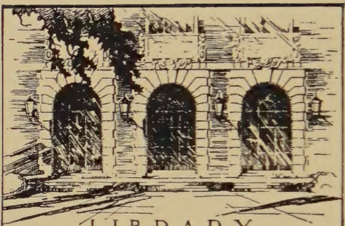

LABORATORY AND FIELD ECOLOGY

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The Responses of Animals as Indicators of Correct Working Methods

BY

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TO

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FOR THEIR UNQUALIFIED SUPPORT OF THE PROJECT AND FOR THEIR AUTHORIZATION OF PURCHASES OF EQUIPMENT DESCRIBED

AND TO

PROFESSOR JAMES M. WHITE,

WHOSE SYSTEM OF DAY-AND-NIGHT CENTRALIZED SERVICE TO MACHINERY MAKES POSSIBLE THE CONDUCTING OF CLIMATE-SIMULATION EXPERIMENTS

CONTENTS

PREFACE

In this book the writer endeavors to present the results of experience in researches aimed first at the discovery of the way and conditions of life of animals in nature and then at their transplantation into the laboratory for scientific control in experiments simulating natural conditions as closely as possible. Such an aim, inasmuch as it differs from that of physico-chemical study of animals as mechanisms under constant conditions, necessitates different equipment. To a large extent, in fact, the organism itself dictates the character of the apparatus to be used. This idea is the main thesis of the present volume and serves as a guiding principle in the writer's treatment of all questions pertaining to the selection, installation, and operation of equipment for the various kinds of climate simulation.

When begun some ten years ago, this book was intended to describe the equipment used by the writer, but it was soon found that this equipment was inadequate and finally that much of it was based on incorrect principles. Accordingly a great amount of pioneer work had to be undertaken, and in order to justify the new experimental methods outlined, a considerable discussion of biological results proved necessary, so that more than half of the book became a presentation of ecological data and results. The incorporation of concepts developed within recent years, together with the improvement of methods made possible by instruments only lately available, has not always been accomplished without sacrificing more or less of the plan which the writer was trying to follow for each part. Consequently the discussion of some topics is, no doubt, out of proportion to their relative importance, but a thoroughly coherent and well-balanced treatment of this branch of ecology is hardly possible at the present stage of advancement of the science.

It is hoped that the book will be useful not only to research workers who will welcome its suggestions on questions of procedure but also to students in general who desire a means of orientation in this comparatively unexplored field. The first six chapters are designed primarily to define the viewpoint of animal ecology and to show the setting of its problems, especially those that lend themselves

to experimental work. Succeeding chapters deal with the relations of organisms to particular factors of the environment and with the methods of measuring and controlling each factor. This plan is varied by the insertion of two summary chapters (Chapter XI, on "Temperature and Humidity in Combination," and Chapter XV, on "Evaluation of Factors Other than Temperature and Moisture, and the Comparison of Species") in which consideration is given to the combined effects of factors previously discussed separately. General plans for buildings and grounds, where the various small units of equipment may be given their proper places, are outlined in Chapter XVI (for terrestrial animals) and Chapter XX (for aquatic animals).

Besides the detailed directions, cautions, etc., given with descriptions of individual pieces of apparatus throughout the text, a number of suggestions to teachers and investigators will be found in the Appendix. These deal with (1) methods of keeping records, (2) specifications for students' tables and other laboratory furniture, (3) plans for sets of equipment based upon a sliding scale of funds available, and (4) lists of names and addresses of firms prepared to supply equipment which is not prominent in biological catalogues. The intention in presenting plans and types of apparatus was not to advocate that made by any particular manufacturer but rather to illustrate correct principles, and in many cases other manufacturers unknown to the writer may make equipment equally good from this viewpoint.

In general, the metric system has been used throughout the text, and all unlabelled formulae are in metric units. However, English units have been used for large pressures, dimensions of buildings, iron pipe sizes, screen meshes, etc., sometimes without equivalents.

Experimental work found necessary to develop and test equipment was financed in part by grants from the Graduate School Research funds of the University of Illinois and in part by the Department of Zoölogy of the same institution. This covered work on the use of photo-electric cells, which was carried out in collaboration with Dr. Jacob Kunz, with the unstinted support of the departments of Physics and Zoölogy. The equipment developed in connection with the work of the Illinois Natural History Survey aided greatly in completing the descriptions both of results and equipment. Drawings for figures 169 to 172 were supplied by the Survey. But for the careful work of Messrs. E. Amelotti, H. J. Anderson, N. H. Barnard,

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V. E. Shelford.

Champaign, April 30, 1929

INTRODUCTION

I. BIOLOGICAL SCIENCES

Biology may be separated into three pure-science divisions capable of independent investigation with the development of independent theories and independent philosophies. In other words it constitutes three relatively independent sciences.

One of these divisions may be called physiology, biochemistry, or biomechanics, for it attempts to interpret organisms in, and reduce life processes to, terms of physics and chemistry. This is strictly a laboratory science and uses the methods and equipment of physics and chemistry, constant conditions, in particular, being required. Natural environmental factors are not a matter of concern.

Another is the division of so-called general zoölogy and general botany, which deal with the plant and animal kingdoms arranged in the supposed order of evolution. Evolutionary philosophy is the background of the study of development, anatomy, and classification. In all evolutionary theory, the environment is considered as a factor in natural selection, adaptation, and extinction; but very little environment-simulation experimentation has been carried on, though the need for such study is obvious.

The third division is that of bioecology, which is the sociology of organisms. It considers them in communities, large and small, which develop, grow and invade new territory, compete, and die. Communities are adjusted to climates; climax communities are climatic.

II. MODERN ECOLOGY

The modern ecology received its impetus from studies of plant and animal communities. Investigation has been stimulated by the concept that law and order govern communities: succession, annuation, aspectation, which are, in fact, the growth of the community and its responses to climate and the rhythm of seasons. The law and order which Warming (947) pointed out in his study of the vegetation of the sand dunes of Denmark was especially important. The fact that natural phenomena in the aggregate of living things were capable of detailed analysis and classification on a dynamic and

genetic basis attracted investigators into the field and considerable progress has been made. This progress is notable in plant ecology in the last thirty-five years. In animal ecology, however, less progress has been made. Here the study of communities is more difficult, and has been under way for less than twenty years. The noteworthy contributions, of which only a few can be enumerated, are such as those of Petersen (669, 670, 671) and his associates (99, 100, 101, 438) at the Danish Biological Station, beginning publication in 1911, and of Murray and Hjort (610) in their report on the expedition of the Michael Sars published in 1910 to 1912. All these workers applied quantitative methods to marine communities. The terrestrial and fresh-water work dates from a somewhat earlier period and was unfortunately not quantitative, though animals were, in practice or by actual notation, classified as scarce, common or abundant.

Adams' Survey of Isle Royal in Lake Superior (1909) is an early example of comprehensive appreciation of modern ecological problems and viewpoints.

In the fifteen or more years since the publication of the various papers noted above, developments have made room for closer delimitation of the subject of ecology than was possible when the writer published his first series of papers on animal communities (1907 to 1915; 802–812).

At the present time there is no need and little justification for the term *autecology* as it has been interpreted relative to animals or for that matter for the use of the term ecology referring to particular species, as very commonly construed. Ecology is the science of communities. A study of the relations of a single species to the environment conceived without reference to communities and, in the end, unrelated to the natural phenomena of its habitat and community associates, is not properly included in the field of ecology. The efforts of ecologists should be directed toward the explanation of community and habitat relations. To this end, experiments of various sorts may be performed in nature. This is a new field of experimentation which it is hoped this book may stimulate (885, 952).

In ecology it is even more true than in work from other viewpoints, that the precision of the laboratory is necessary. Furthermore, this precision can not be attained by ignoring factors that are not especially under consideration as is common practice in various other types

of laboratory research. The various factors of natural environments must be studied and duplicated so far as possible, as well as varied.

The habits and responses of organisms in their natural environments afford the foundation for determining the kind of experiments to be performed and the kind of equipment to be used in ecological (and climatological) experimentation. The initial facts are usually discovered in course of the study of organisms in nature. In other words, nature supplies the problems to be solved in the field and laboratory experiments.

III. RESPONSE IN NATURE AND EXPERIMENTS

The responses of individuals in communities fluctuate greatly with climate and weather rhythms and irregularities. This fact demands climate-simulation experiments in order to determine the rates of development, rates of reproduction, survival, and other factors which have to do with the success and abundance of a species under various variable conditions. Conditions in water operate similarly to climate on land, and *subaquatic climate* is a term which it would be well to introduce quite generally. Climate is the sum total of weather at a particular point and hence it is essential to have accurate records of daily and even hourly changes in weather conditions.

Ecology considers not only the relations between organisms in a community made up of different species, but also the relations of each species to its environment as a whole and to each of the conditions which make up the environment. Species often live in places where the climatic or hydrographic conditions are greatly modified by organisms, so that the experimenter cannot consider climate alone but must also consider other organisms and objects.

In applied science, especially in entomology, the necessity for the conducting of climate-simulating experiments is ever growing in importance. This is an outgrowth of the oldest of all biological sciences, namely, phenomenonology, or phenology. Although phenology has been greatly altered by modern experimentation and needs to be corrected still more, it has made some important contributions to our main field of interest.

IV. ORGANISMS AS INDICATORS AND PHENOLOGY

The use of organisms as indicators of the suitability of soil and climate, pollution, etc. which has been developed recently, and the almost simultaneous revival of their use as seasonal indicators make a recital of the history of the subject cogent at this point.

The earliest science was no doubt concerned with the correlation between periodic phenomena such as the flowering of certain plants and the arrival of migratory game or important birds. Primitive men doubtless were guided by these events in securing food and clothing. Plants and animals were thus early used as indicators. Calendars of periodic events are among the early records of biology and agriculture. Becquerel (1853 (69)) published extracts from agricultural calendars, the earliest of which is the Chinese calendar of 700 B.C., having to do with the Hoang Ho Valley. He compared this with a Roman calendar of 45 A.D., an Arabian calendar of 870 A.D., and a European calendar of 1551. Marked differences were evident in the time of the same event at different longitudes in the same latitude. In the half century following the work of Linneus (1751), a number of Swedish, German, French, and English calendars were produced. In the nineteenth century there was much work done in both Europe and America. Phenologists early sought some means of estimating the amount of progress toward a particular periodic event in advance of its occurrence. Their efforts were thus directed toward correlating periodic events with meteorological conditions. Among the earliest efforts are those of Reaumur (1735 (715)). He is commonly credited with being among the first to "sum" temperatures though Candolle (145) is most often cited. Some of the earlier investigators deducted temperatures representing the starting point of development from the various readings, so as to utilize only "effective" temperature in making up the sum. This subject has received much attention. Various European workers have carried on careful critical studies, employing various detailed methods for determining the total accumulated temperature necessary to bring a given plant into bloom or to ripen a crop of grain. It was, however, soon discovered that the sum of temperatures for the same stage of development of the same variety of plant varied a great deal from season to season and from year to year. Consequently, this method fell into considerable disrepute, though its influence on modern biological concepts is important.

There were, however, other purely phenological observations. In 1830, Schu er (fide Hopkins (408)) found that between Parma SCHUBLER in Italy and Greifswald in Prussia periodic events were later in spring by four days for each degree of latitude and for each 100 meters altitude. Fritsch (314) found a difference of four-tenths of a day for each degree of longitude, earlier westward. Oettingen (629) has said that physiologists know only how to destroy phenology as they do not know anything to put in its place.

Hopkins (408) published the results of years of observations on various plants but especially on the ripening of wheat. He formulated his "bioclimatic law":

> Other conditions being equal, the variation in the time of occurrence of a given periodic event in life activity in temperate North America is at the general average rate of 4 days to each degree of latitude, 5 degrees of longitude and 400 feet of altitude; later northward, eastward, and upward in spring and early summer and the reverse in late summer and autumn.

There are certain general relations between this hypothesis and Merriam's life zones.

V. EXPERIMENTS AND ENVIRONMENTAL INSTRUMENTATION

The discovery of important organisms, namely, those showing responses to climatic fluctuations, and of certain essential relations to climate and weather, is necessary to intelligent experimentation. The purpose of laboratory experiments, when applied to problems concerned with the effects of climate and weather upon plants and animals is primarily to make possible the correct interpretation of the responses apparently correlated with the various weather factors and their variation. The point of view is altogether different from that of meteorology, which deals with the physics of the air. Meteorology places its instruments where the general conditions can be determined, while biology and climatology would place them where the organisms of interest are located. In practice, instruments in animal habitats should be compared with those under standard meteorological conditions. The responses of organisms are of primary interest to biologists. The conditions to be measured and simulated in experiments are those which influence the rate of growth, length of life, fecundity, abundance, death rate, or time of appearance. In other words the *responses of organisms dictate the kind of instruments, methods and equipment* to be used in observations of the general

environment and in experiments. The habitat of the animal determines where the field instruments should be placed and the kinds of conditions which may be regarded as normal to the species under weather conditions usual for its geographic range (Hann (370)).

a. Controls

Controls are of two kinds, normal and experimental. In a normal control the aim should be to maintain conditions as nearly natural as possible. Outdoor conditions are best, provided the season is nearly normal; when it is not, a modification of outdoor conditions is desirable.

Experimental controls have all conditions the same as in the experiment except for one or more factors, the effects of which it seems desirable to determine. Thus, two experiments may be set up with exactly the same equipment and conditions of temperature, moisture, movement, etc., but with different degrees of illumination, in order to determine the effect of light. If one container were kept dark, it might be called the "Experimental Control." Both it and the illuminated container should be compared with the normal control.

b. Variable conditions in experiments

One feature that is necessarily introduced into experimental climatology and ecology is *variability*, approaching the variations from hour to hour. This involves all weather factors. Some, however, vary together either inversely or directly. Temperature and humidity vary inversely; changes in temperature are nearly always accompanied by changes in humidity in the reverse direction. The two are changing almost continuously from hour to hour. Light and temperature vary together directly, but not with the same close correlation as do temperature and humidity. Light increases with the advance of the day, following a minimum light and a minimum temperature, which are not coincident. Light and temperature commonly increase together to mid-day. The maximum temperature usually comes about two hours later than the maximum light. The temperature always lags behind light in clear weather.

It thus becomes evident that our knowledge of the organisms to be experimented upon is the basis for pre-equipment for the experiments. Equipment can, however, be planned to conform to our general knowledge of organisms. It is the purpose of this book to

outline the equipment and methods which conform to present knowledge of the responses of animal organisms in general.

The use of organisms to indicate what conditions are needed in experiment is illustrated by the following facts. It has been found that the effects of variable conditions are different from the effects of constant conditions. Under variable conditions, development is from 2 to 10 per cent faster than under constant conditions. Moving air gives results different from those in still air. Many such general examples could be cited. Special methods adjusted to the life needs of animals are as numerous as the animals themselves. In spite of this fact, certain general principles can be laid down. The statement of these general principles constitutes the chief purpose of the succeeding chapters. They do not purport to serve as a guide for physiological study, or to aid in the experimental work of those aiming at the analysis of the organism in terms of physics and chemistry, though it is by no means sure that such methods will not be of much importance in these investigations in the future.

Equipment available for the type of work described herein is constantly changing, usually improving, but from time to time certain types of equipment are discontinued. No equipment can accordingly be described or recommended except on the basis of its service as illustrating correct principles dictated by the characteristic responses of organisms and the normal variations of conditions in nature.

c. *Undesirable policies of the past*

The tendency to imitate the methods of physical and chemical laboratories in the use of constant conditions only, i.e., the failure to run simplified variable-temperature (humidity, etc.) experiments and to conduct outdoor observations, should be discouraged in ecological work. The tendency among investigators with ecological interests to select animals for general study which have no important relations in communities or whose relations are unknown is to be deplored. When this is done haphazardly, "autecology," natural history and physiology are put ahead of synecology, which is the new science and should afford the guiding principles for the study of particular species. In general there has been too little study and recognition of synecology. Animal ecological study has been too strongly influenced by the methods of the older fields of biology in which specialization on a small group of species was regarded as highly desirable if not essential.

CHAPTER I

Some Problems of Ecology and Climatology

I. INTRODUCTION

Ecology and climatology are concerned with the relations of biotic communities (or particular organisms representative of communities) to weather, climate, physiographic and hydrographic conditions, and to each other. Some of the problems are obvious, such as relative abundance of individuals in different years. The outbreaks of locusts, the mouse plagues, changes in abundance of fishes, etc., have been noted throughout historic times but have never been adequately investigated or fully explained. Modern entomology, plankton study, mammalogy, and ecology have discovered more fluctuations. The need for the application of sprays and studies of the acclimatization and success of domestic animals has led to detailed studies of certain domestic species and of certain insect pests. This has supplied much information about particular species.

The use of climatic diagrams has brought out some correlations of weather, climate and particular factors with the success of particular species, but in many cases the confirmation of the conclusions as to which factors are primarily responsible awaits experimental work. Factors go in groups or pairs, one being so often correlated with another that failure to judge as to the right factor may be frequent. This is illustrated by the writer's experiments (with Powers) with the reactions of salmon (833). Salmon were supposedly guided to fresh or salt water by salinity. Young salmon secured in the sea would supposedly select salt water instead of fresh. However, when the experiment was tried they paid no attention to differences in salinity, but were found, on further investigation, to be reacting to hydrogen ion concentration or its correlates other than salinity. Differences in hydrogen-ion concentration nearly always accompany differences in salinity, but under certain conditions this might not be true, so that the taking of salinity would not be significant.

It is necessary in all cases to know the sensibility of organisms to particular factors. Graphic methods such as those introduced by

Ball (55) permit the tentative determination of the apparent weather factors governing abundance, etc. Graphic methods may also be profitably used in studies (448) of areas of abundance, favorable and unfavorable years, critical periods, efficiency of reproduction, milk production, food storage, etc. We do not accordingly rely upon experimental work to determine the responses of organisms. Observation if carried on continuously, in correlation with records of conditions, early suggests what the responses to a given set of conditions may be. If this process is carried on over a long period, e.g., a century, even much less, it will perhaps give more important results than a large series of experiments. The object of modern science is to get the best results in the shortest time, and with greatest accuracy. To attain this end present experience in the field indicates that *observation must lay the foundation for experiments and thereafter the two must go on together.*

II. CYCLIC PERIODICITIES

1. Weather

Many variations in weather from year to year fall into cycles (14, 388).

a. Solar radiation. Since 1902 measurements of solar radiation have been carried on at various places. The Smithsonian Institution (2) is making observations at Mt. Harqua Hala, Arizona, and Montezuma, Chile. In 1917, Clayton (168, 169) published data indicating close correlation between solar radiation and atmospheric conditions (411). In 1920 the same author showed how the temperature in Buenos Aires is intimately related with solar radiation: (a) Changes in temperature occur at definite intervals after changes in solar radiation. (b) At times of greatest solar activity a change of 1 per cent in solar radiation is followed by a change of 1.4°C. in temperature. (c) Means of solar radiation and of temperature showed $6\frac{1}{2}$ and 13-day periods.

Sir A. Schuster (for method see (786)) reviewing data on sun spots from 1620–1900 found (1) a period of 11.125 years and (2) periods of 8.34, 4.76, 13.6, and 33.375 years.

b. Temperature. Koppen (490, 491) was an early student of temperature periodicities. Mielke (596) related them to sun spots. Arthur Wagner (934) using temperature data from Vienna and middle European stations, extending over 143 years, found a 16-year period.

c. Rainfall. Clements (34, 174, 175, 176, 260, 261, 262, 263) has made many applications of western United States rainfall data in the interpretation of the vegetation. Alter (34) using rainfall records of Northern Europe (173 years), for eastern United States (103 years), and for western United States (73 years), found evidence of a fifteen-year period.

d. Cloudiness (388) (945). There are fluctuations in amount of sunshine due to cloudiness. Increased cloudiness usually, though not necessarily, accompanies increased rainfall.

e. Dust. Dust cast into the air by volcanic eruptions shuts out radiation with pronounced effects. Redway (716) has shown the effects of dust which followed the various great volcanic eruptions. These periods are characterized by unusually cold weather. They interfere with the otherwise normal periodicities.

f. Other irregularities. There are many irregularities which have not been explained which at the same time are important to life of all kinds. In addition there are relatively small areas where rainfall is unusually great or small compared to surrounding territory. All these as well as the other periodicities and irregularities are of the greatest importance in determining the responses of organisms to weather and climate and are the basis for the planning and interpretation of experimental work.

2. *Biological*

a. Harvests. W. H. Beveridge (82) applied Schuster's method of periodograms to data on wheat prices of the years 1500 to 1869. These prices were collected in forty-eight different localities in Europe. The price of wheat is a good indicator of the harvest conditions prevailing during any year. The probability that such fluctuations as occurred were due to random sampling is on the order of 1 to 2,500,000. Peaks occurred every 15 years from 1678 to 1846 and every 30 years from 1556 to 1678. Minor cycles of 4.37, 5.11, 3.71, and 2.74 years were evidenced. (888.)

b. Tree growth (260–263, 493, 1,000). The annual rings of trees may be made to furnish evidence as to the climate of years past. There are three types of evidence in trees examined by Douglass (260–263): (1) direct correlation between rings of yellow pine and rainfall such as that noted at Prescott, Arizona; (2) resemblance in individual rings over a wide extent of country where climate is the

only common factor; (3) similarity in ring variation over large areas —California, Arizona, and Colorado. Mean sensitivity equals the difference between each two successive rings divided by their mean. Large crops of young trees appear only periodically.

c. *Insects* (946). Cycles of abundance of insects have frequently been noted. For example, the chinch bug has long been recognized as an "epidemic" pest (Riley (741)). Cycles and irregularities in the abundance of grasshoppers were discussed by Thomas (891) in 1878 (916, 917). There were twelve years (1914 to 1926) between two summers of unusual abundance of the codling moth in Illinois,

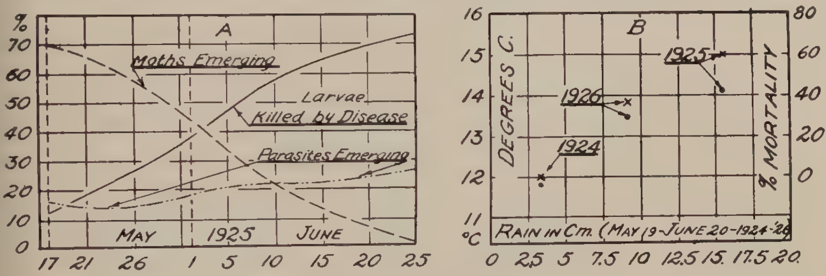


FIG. 1. Showing the relation of disease, parasites, and weather to mortality of the redbacked cutworm in Saskatchewan.

A. The percentage effective infection throughout the season by parasites and disease as occurring under field conditions in 1925. Emergence of parasites was decreased by death of hosts from disease (after King and Atkinson (475).

B. The correlation between weather and mortality of larvae from disease during a brief period in 1924, 1925 and 1926; the dots indicate rainfall and temperature on the coördinate scale; the x's indicate mortality on the right hand scale (from data by King and Atkinson (475).

and the weather conditions were very similar in the winters preceding these two summers (Shelford (826)). In the case of the codling moth this was probably a direct response to favorable and unfavorable weather conditions in which the favorable year is similar to that of the average European weather. Frequently predators, insect parasites and disease play a rôle. Insect parasites and predators act in a more limited regulatory fashion than disease, tending to preserve a balance. When such a balance is destroyed and the host species increases greatly, due usually to abnormal weather conditions, disease often plays an important rôle in reducing the numbers. The greater potency of disease under such circumstances is shown for the red-backed cutworm in 1925 as reported by King and Atkinson (475). Figure 1, *A*, shows the potency of disease as recorded by

these authors. It was estimated that if disease had not occurred the insect parasitism would have amounted to approximately 61 per cent. The correlation between disease and rainfall in the red-backed cutworm in Saskatchewan as determined by these authors is shown in figure 1, *B*. The biotic control is here as probably elsewhere largely under control of weather.

Seamans (790) has shown the correlation between the abundance of the pale western cutworm and wet weather in May and June; he attributes this mainly to the action of parasites, rather than disease though this latter factor is considered of greater importance by Cook (202).

Concerning the pale western cutworm, Seamans (790, see also 647) makes the following statements:

> A long series of observations have brought out the following: If there are less than ten "wet" days in May and June it is probable that there will be an increase in the number of cutworms the following year.
>
> If there are between ten and fifteen such days in May and June there will be, in all probability, some *decrease* in the number of cutworms the following year.
>
> If there are more than fifteen such days in May and June, little trouble may be looked for from this insect the following year.

The observations indicate that the response of insects is sufficiently rapid to cause outbreaks or great abundance or scarcity of individuals which may be due to weather of a local area or to wetter or drier years or months which may fall anywhere within the eleven- and fifteen-year periods noted above.

d. Birds and mammals (208, 276, 277, 298, 300). It is shown in a number of ways that the earth's climate varies periodically corresponding to development of spots on the sun. The average period between sunspot maxima is about eleven years. There are periodic fluctuations in numbers of many animals, which can be related to climate. Diseases and parasites have been considered important in these fluctuations (277) but lack of quantitative work on the diseases and parasites leaves much of this discussion in the field of speculation and conjecture.

Lemmings in Norway periodically migrate in great numbers from the arctic-alpine tundra of the mountains to the lowlands. There has been a lemming migration every three to four (average 3.6) years. Lemming maxima in many countries correspond closely to those in Norway.

Rabbits (276, 368) (varying hare) have a ten-year period between. maxima numbers, corresponding partially to sunspot minima (fig. 2, after Elton (276)).

Mice (52, 509, 679, 680) have maxima corresponding to lemmings. In England mouse plagues recur about every eleven years. It is suggested that a sunspot climatic cycle reinforcing a shorter period is necessary to produce numbers sufficient for plague.

Carnivorous animals (both mammals and birds) tend to have 11-year period or 3½-year period depending on whether their chief food is rabbits or mice and lemmings. Frequently periods of both lengths can be detected in records of abundance of a species (figured from skins taken by Hudson's Bay Company).

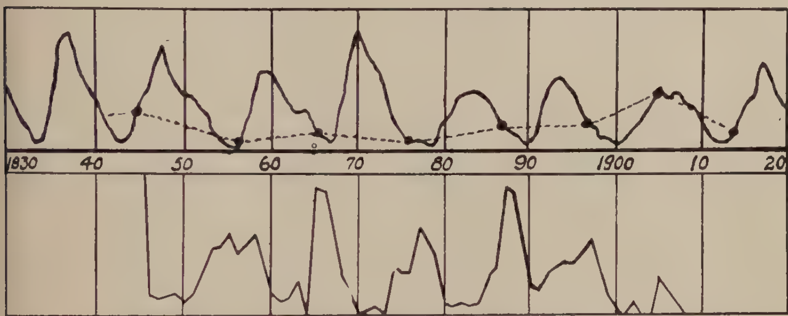


FIG. 2. The upper curve shows years of maxima of the varying hare in Canada, marked on the sun spot curve by black dots. (After Elton (276) who explains the discrepency of 1905 on the basis of volcanic eruptions which contributed to the lowering of the earth's temperature.) The lower figure shows the number of varying hare skins taken annually by the Hudson's Bay Company.

In years of abundance there are more individuals in a brood, and more broods than in bad years.

Beaver does *not* show periodic fluctuations (because it eats bark and is not dependent on yearly crop).

Birds fluctuate in numbers. Pallas' sand-grouse, from central Asia, invades England about every 11 years.

Variations in rainfall are great (Clements (176)), but those of other meteorological factors at sunspot maxima and minima are very small when measured directly. Fluctuations in numbers of animals show corresponding variations on exaggerated scales.

III. ANNUAL CYCLES

Various systems by which the dates of occurrence of any natural life rhythmic activity may be predicted for any particular location have been devised; the most recent one is by Prof. A. D. Hopkins (408). It is based upon the old science of phenology or the records

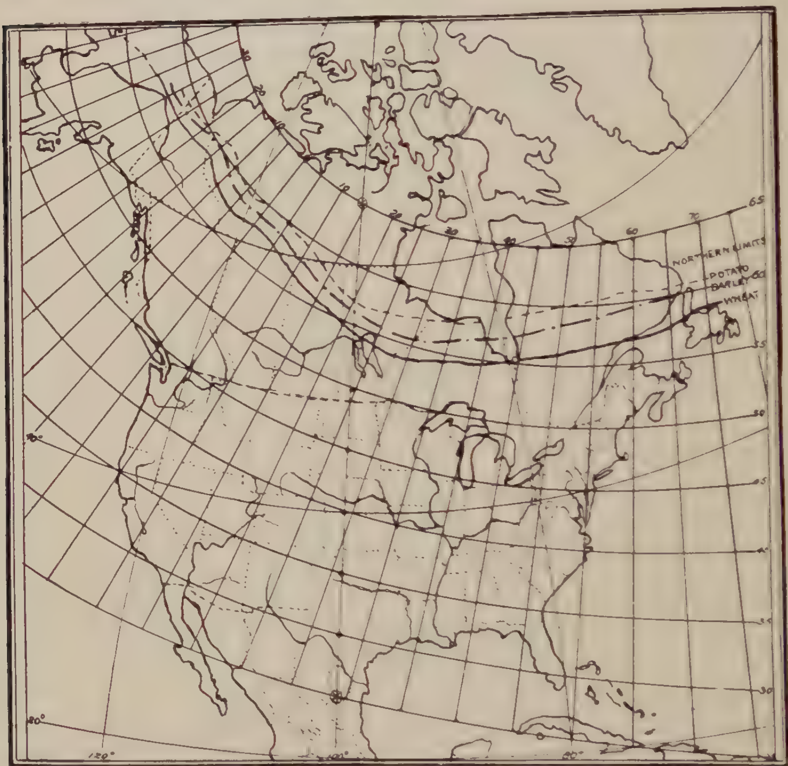


FIG. 3. The Hopkins (408) isophenal map. Every fifth isophenal meridian and parallel is shown. The parallels are laid off as actual degrees on the 100 degree meridian from Greenwich.

of occurrence of periodic events in living organisms, such as the leafing of trees, flowering of plants, etc. Hopkins states his bioclimatic law as already given on p. 5. There are, however, always departures from the theoretical time constant and these are determined by observations at each particular locality and corrections

made for them. He has devised a system of isophenal maps (fig. 3), map calendars, and adjustable and computing calendars and tables. By the aid of these he computes the time for any natural life activity, providing it is definitely known for one locality.

An isophenal map was prepared with isophenes drawn through equal-event dates at the same altitude. These slope from northwest to southeast. Their positions and numbers correspond to latitude on the 100th meridian. The isophenal meridians are perpendicular to the isophenes and pass toward a pole in the region of Iceland. This work has served as a basis for determining the Hessian fly-free dates for sowing wheat. Wooster, Ohio, was used as a base for observation. The important principle introduced into agricultural practice here is the establishment of a *base* for observations. The work has been applied chiefly to the prediction of dates at which the Hessian fly will cease emerging and go into hibernation. The application of the system in several states has shown that more bases are necessary.

The simple use of the isophenal maps and Hopkins' law has proved a rough guide in some states in average years. Prof. T. H. Parks (652) of Ohio State University has investigated fly-free dates in detail and states in a personal communication that rainfall and temperature cause variations from the base observations not to be expected according to the law. This would result in erroneous predictions.

The results of several years of close observation are combined into a map for Ohio. The isophenes are parallel to latitude and no account is taken of elevation as in Hopkins' chart.

Improvement of such maps may be brought about by: (1) longer and more detailed observations on both weather and events, to show causes for variations; and (2) experiments to determine factors which cause the variations.

The correlation of seasonal events is only one phase of ecological study to be carried on without experimental analysis. There have been various attempts to correlate general distribution with general conditions. One of these, the "life zone" work of Merriam (591), has found considerable acceptance in the United States and Canada, especially among the ornithologists. This work originally attempted to correlate the distribution of life with temperature. Whatever merit or lack of merit it may have, it gives a purely static outline of

the supposed relations of animals and plants to one feature of climate, namely, temperature. It does not proceed to further analysis of the cause of the presence of the organisms or of their dynamic relations. It does not consider some organisms as important in the control of the communities, and it has applied neither experimental methods of any kind nor quantitative field methods.

IV. THE RELATION OF PARTICULAR SPECIES AND GROUPS TO WEATHER AND CLIMATE

1. Man (disease)

Huntington (420) has pointed out that the principle of the new tuberculosis treatment is the ecological idea that the respiratory system requires outdoor air. Most important conditions are: light, air purity, temperature, relative humidity, and variability. The old treatment centered around temperature. The new treatment centers around variability. Statistics show that the death rate from pneumonia and influenza in New York varies inversely as the temperature. In general, deaths are fewer when the humidity is high than when it is low, and decidedly less when the temperature is falling or rising than when it is uniform. Data on epidemics of influenza show that the same factors serve to increase or decrease the severity of the epidemic. The human body seems to have an optimum of temperature, humidity, and variability. The ideal air is (1) variable in temperature, (2) fairly moist, (3) not too warm, air like that which makes October and May the most healthful months of the year. Fluctuations of bacterial activity may have an important relation to disease. Further work is required to determine the optima for mankind and for disease-producing bacteria.

2. Sheep

Domestic sheep were made the subject of a detailed study by E. L. Johnson (448) whose results illustrate the general methods of study of wild and domestic animals by the use of climatic diagrams. Diagrams of climate and climatic relations are of two types: (1) Those referring to localities and showing mean quantitative meteorological data by months or other suitable periods, covering two factors, plotted on coördinate paper. The points representing the conditions of the two factors under consideration are connected ~~together~~ to give an irregular figure (fig. 16, p. 24). The other type (2) is based

FIG. 4. The distribution and numbers of domestic sheep indicated by the density of stippling (after Finch and Baker (290))

upon the response of the organism under consideration to combinations of two factors; the factor chart is abstracted and the data are usually plotted on this chart. The second type is fully discussed in Chapter XI; figures 119 and 130 illustrate the principle. In the present chapter, attention is devoted to the first type only. Ball (55) working in Egypt, plotted mean monthly temperature and humidity for various oases with a view to determine their suitability as winter health resorts. Taylor (881) plotted the climate of several localities of the world especially Australia, in the form of mean monthly wet-bulb temperature and humidity. He called his diagrams *climographs.* In 1919 he published another paper (882) and similar temperature-rainfall diagrams which he called *hythergraphs.* He also presented certain generalized *limits* diagrams for the climatic regions of Australia and compared them with the monthly means of localities in various parts of the world. From these comparisions he concluded what crops were suited to the Australian climates. He thus laid down the principle of the generalized diagram for comparison.

Johnson (448) analyzed climate in three principal steps as suggested by (a), (b) and (c) below. His work is introduced in detail to show methods of analysis rather than to bring out the relations of sheep as distinguished from other animals.

(a) Areas where the species is abundant have a suitable climate. (b) Critical periods of the life history determine whether a climate is suitable or not. (Critical periods are associated with reproduction.) (c) Favorable and unfavorable years and months confirm the conclusion based upon general climate.

a. Distribution and climate. Figure 4, shows the distribution of domestic sheep in various parts of the world (290). There is dense sheep population in some localities and none in others. The areas of dense population have similar climates. The ideal climates here represented for sheep (fig. 5) are based upon these dense centers. It has been assumed that sections having a dense sheep population have favorable climatic conditions for sheep production. Such dense world centers exist in South America (Uruguay and northeastern Argentina), South Africa (Basutoland), Australia (New South Wales), New Zealand, Great Britain, European Turkey, and Bulgaria. Russia and the United States also have a large sheep population.

The climatic factors to be considered are temperature, rainfall, and

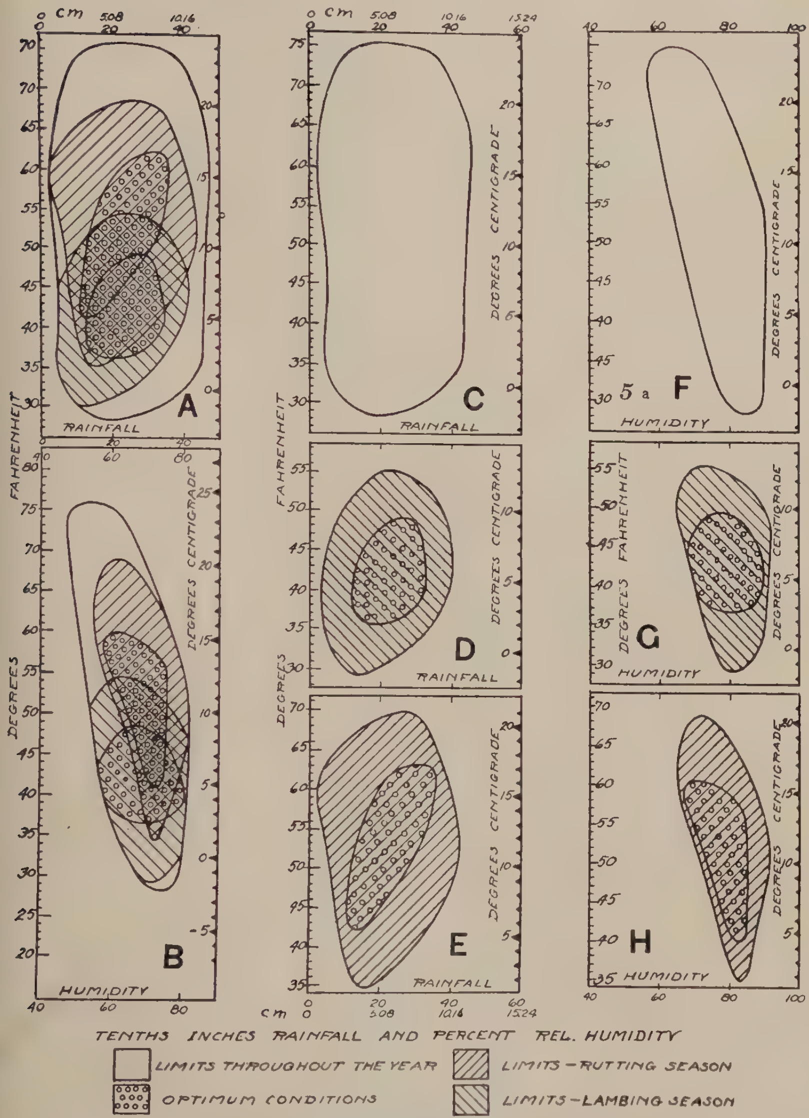


FIG. 5. *A* and *B*, composite hythergraph and climograph of dense centers of sheep population in the world; *C* and *F*, limits for the year; *D* and *G*, for the lambing period; *E* and *H*, for the rutting period (from 448).

humidity. Comparisons were made by the use of the hythergraph (temperature-rainfall) and the climograph (temperature-humidity). Graphs were made from the mean monthly temperature, rainfall, and humidity records for various meteorological stations located in sheep-growing sections. Each point on the hythergraph represents the mean of the temperature and the rainfall for a particular month. The points for each month in the year were plotted and then connected. For the climograph the mean monthly temperature and humidity were used. By this method two factors and the months or critical periods can be shown at one time. In these graphs the temperatures are represented on the vertical scale to the left, and the tenths of inches of rainfall and the per cent of relative humidity on the horizontal scale at the top. When possible, records from several stations with averages over as long a period of years as possible were selected for each section.

These graphs, representing the mean monthly temperature, rainfall, and humidity of the most important (densest) sheep centers in the world, were made into a composite graph, by tracing one graph on top of another and by connecting all the outer points (fig. 5, *A* and *C*). The climates are mild with rainfall sufficient for good forage; and humidity considerably lower in summer than winter.

On the composite graph the rutting and lambing seasons have been plotted because sheep seem sensitive during these periods. The lambing season, which extends over three or four months, was obtained for each country and then plotted. The middle month (or months) was taken as a mean because the bulk of the lambs are born at that time (fig. 5, *A*, *B*, *D* and *G* (448)). The rutting season was determined from the lambing season by counting back five months (fig. 5, *E* and *H*).

The lambing and rutting seasons fall within comparatively narrow limits of temperature, rainfall, and humidity, and within narrower limits than does the composite graph for the whole year.

The graphs made from sections which have less dense population than those from which the composite was made show some variations—the climate may be hotter in summer, colder in winter; it may have more or less rainfall, a higher humidity, or a combination of these factors. The lambing or rutting seasons may not fall within the limits of those in the composite.

b. Critical periods. The periods in the life of a sheep during which

it is more easily and more seriously affected by unfavorable conditions are the lambing and rutting seasons, which, as stated above, fall within narrower limits of temperature, rainfall, and humidity than

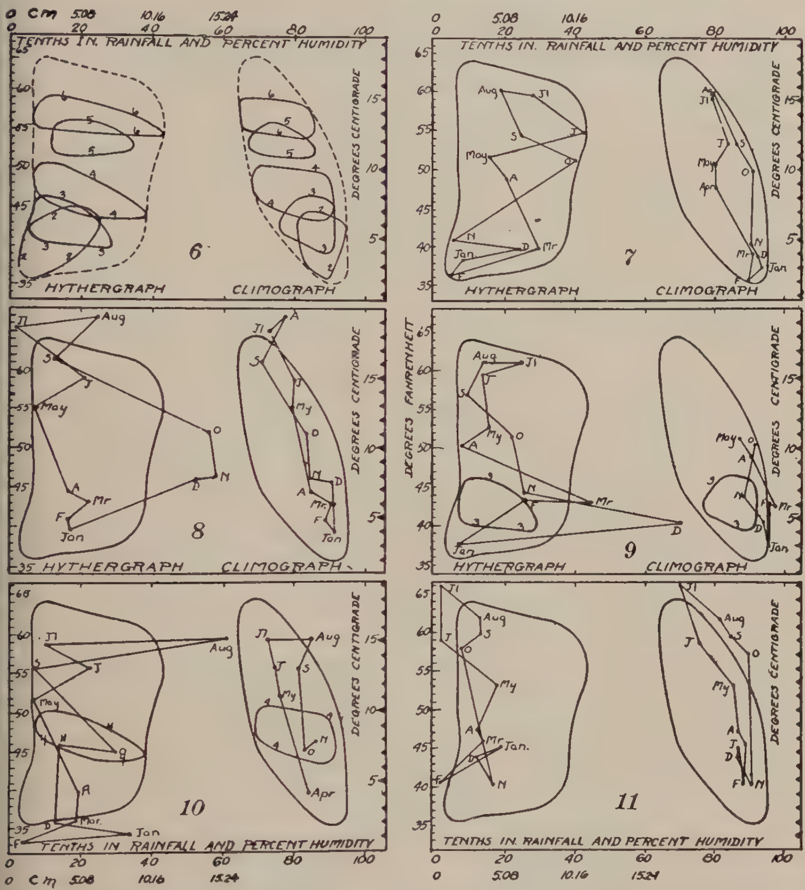


FIG. 6. The limits for February, March, April, May, and June of a good sheep year in England.
FIG. 7. Good year, Reading, England, 1909.
FIG. 8. Bad year, Hastings, England, 1911, due to high temperature and humidity during July and August.
FIG. 9. Bad year, Reading, England, 1914, due to wet March and December.
FIG. 10. Bad year, Rounton, England, 1917, due to cold spring period of critical months.
FIG. 11. Bad year, Croydon, England, 1921, due to lack of rain, high temperature, humidity in summer (from (448)).

the general conditions under which sheep live. The first few months of the life of a lamb and to a less degree of the time of pregnancy are also critical periods (fig. 6). A successful lambing season is often interfered with by cold, wet, or snowy weather, or by a shortage of feed. The new-born lamb is not able to withstand too rigorous climatic conditions. Likewise, the ewes, if exposed to excessive rainfall, or large amounts of snow, or if there is a shortage of feed, are liable to come to lambing time in unthrifty condition and give birth to weak lambs. If conditions are extremely unfavorable, atrophy of the fetus, due to undernutrition, may occur.

The growth of the lambs during the first few months is readily retarded by hot, humid weather or by cold, wet weather. The extremely hot, humid weather also causes many lambs to lose weight (figs. 17 and 18). The late-born lambs are more severely affected than those born earlier.

The rutting season comes with a falling temperature. It may be delayed by hot weather, particularly by warm nights. In Tennessee, where climatic conditions are generally favorable for lambing during the winter and early spring, the sheep men find it difficult to get their ewes bred early enough in the fall for early spring lambs. In Illinois in the cool summer of 1915, ewes came in heat during all the summer months, and the first lambs were born in November. The cold, wet weather is very trying to the ewes and lambs; and frequently a cold, wet fall and winter are followed by a small fall of lambs.

c. Good and bad sheep years. Studies have been made of a number of years in south-central England and at Urbana, Illinois, showing that the seasons have considerable influence on the growth of sheep, particularly during their first year. Johnson attributed most of this to rainfall, which he correlated with the weight at the end of the first nine months of the life of the lamb.

The years 1909 to 1921 (1912 no data) in England were studied, and the information regarding the effect of each year upon the sheep was obtained. The years most favorable and unfavorable for the Southdown and Hampshire breeds were selected, also the seasons unfavorable for others in most districts in England. A number of meteorological stations were selected in south-central England, the native home of these breeds and the locality in which they are found in greatest numbers. Climographs and hythergraphs were made from the monthly means for the years 1909, 1910, 1911, 1914, 1915,

1917, 1918, 1919, and 1921. From the information at hand, the best lambing seasons and the most favorable summers, autumns, and winters were selected. From these were made a composite hythergraph and climograph, which represents a good sheep year in England. The unfavorable years can be compared with this good year and the contrast noted (figs. 8, 9, 10, 11 (448)). As the critical months of a good year fall within narrow limits, a graph was made for February, March, April, May, and June of the good years (fig. 6). For example, too cold an April of any given year, when compared with the composite hythergraph and climograph, might fall within the limits of a good year; but when compared with a composite containing the limits for April of a good year (fig. 6) it falls far below (fig. 10). A composite was made for the five months only because they fall within narrower limits than some other months in the year, and come at more critical periods. The graphs for several years differ considerably, and do not always fall within the limits of a good sheep year for England. One critical month may be bad and others good. The graphs for 1909 at Reading, England, fall within the limits of the composite for a good year. That year was satisfactory for sheep and in particular for the lambing season (fig. 7).

The following cases serve to illustrate bad years due to unfavorable critical months and to poor food and water supply. The summer of 1911 at Hastings was hot, and July was very dry; the humidity was high at the time of high temperature in July and August; and October, November, and December were very wet (fig. 8). This was noteworthy because of the small number of twin lambs, the failure of food crops, and the low price of mutton. From figure 9 it appears that March, 1914, at Reading was too wet. Early lambs were weak and mortality was heavy. December of the same year was exceedingly wet, and ewes lost weight. April, 1917, at Rounton, England, was too cold, as were January, February, and March. There was a difficult lambing season with a small lamb crop, but the later months were better. August was too wet, with over 6 inches of rainfall, but the humidity was not high. In 1921 at Croydon the lambing season was favorable (fig. 11). The summer was particularly dry, accompanied by humidity a little above the limits. Water had to be carted for livestock for six months.

A comparison was made between the good and bad years at Urbana, from 1906 to 1922 (figs. 12–15). The rate of gains made by

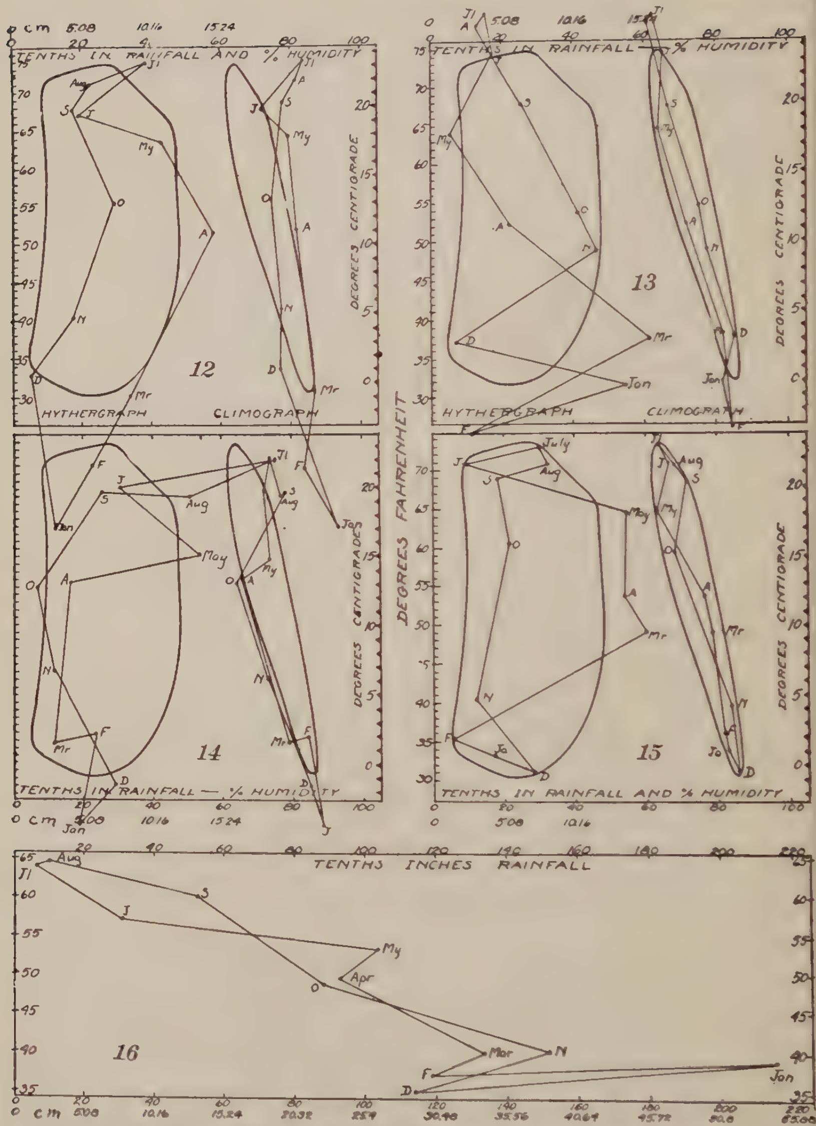


FIG. 12. Bad year, Urbana, Ill., 1912 due to high summer humidities.
FIG. 13. Fair year, Urbana, Ill., 1913, due to low summer humidities.
FIG. 14. Bad year, Urbana, Ill., 1915, due to high humidity and rainfall.
FIG. 15. Good sheep year, Urbana, Ill., (beginning June) 1920.
FIG. 16. Hythergraph, 1919, Cedar Lake, King County, Wash. (from 448). No sheep are recorded in this locality.

the lambs was taken as an indication of the effect of the summer conditions upon them. The mean weights of each breed—Southdowns, Shropshires, and Rambouillets—were plotted for the years 1907, 1911, 1913, 1915. The weights were taken each month, and twice a month during some years. The mean temperatures and humidity for two-week periods were also plotted. Hammond has shown the normal growth of lambs to be regular. Figures 17 and

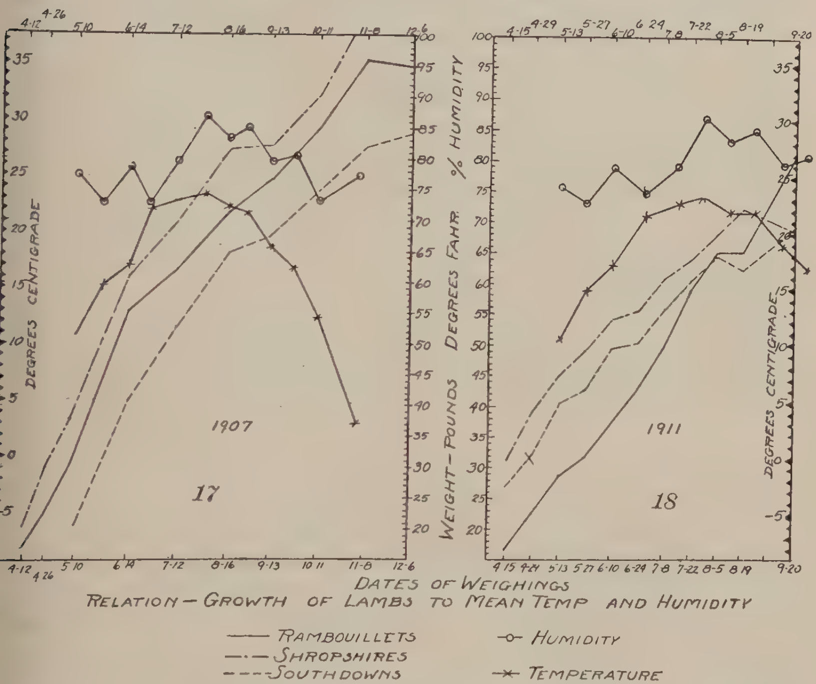


FIG. 17 AND 18. Growth of lambs at Urbana, Ill., 1907 and 1911. (from 448)

18 show a comparison of the growth (increase in weight) with the mean temperature and humidity. The irregularities indicate that a high mean temperature accompanied by high humidity is correlated with the retarded growth of the lambs. In some cases there was a loss in weight during a two-week to four-week period. The graphs presented here (together with others on file at the University of Illinois) show that retarded growth follows high temperature and humidity regardless of the date or the age of the lambs. Curves

drawn for 1913 (on file at the University of Illinois) show comparatively uniform growth of lambs (fig. 13). The difficulty in making use of the weights of the university flock grew out of the different dates of lambing, evidently influenced to some extent by the weather condition of the preceding mating season. Mean growth was rendered insignificant by this irregularity, and retardation in growth was noted at adverse periods regardless of the age of the lambs.

A mean relative humidity higher than 80 per cent and a mean temperature higher than 70°F. seem to be detrimental. The sheep can stand a rather high mean temperature if the mean humidity is not over 60 or 65 per cent. The rate of growth was more uniform in 1913 than for the other three years plotted. The study has not been carried far enough to give definite limits of temperature and humidity. The Rambouillets, which come from a country where the temperature runs higher than it does in the section from which the Shropshire and Southdowns come, seem to be less affected by unfavorable conditions.

Controlled experiments on the growth of lambs under different conditions would be much better for comparison with these records. In fact, such studies are essential to intelligent climatic experimentation. (940).

3. *Other mammals*

a. Mouse plagues (452, 679, 680). Other studies of mammals have been concerned chiefly with mouse plagues. As has been noted, rodents of this group undergo enormous increases from time to time. Among some of the tundra species, especially the lemming, fluctuations in numbers may have taken place in essentially primeval conditions.

Parkes (649, 650) has discussed the importance of nutrition, pointing out that good nutrition favors complete ovarian functioning. He also points out that prenatal mortality occurs in mice. Johnson (452) has summarized the condition relative to mouse plagues as follows:

(a) Conditions known to be favorable to increase of mice are mild winters or a covering of snow, dry springs, and wet summers and falls (or irrigation) to provide abundant vegetation for food and shelter. (Elton (276), Lantz (509); Piper (679, 680).

(b) Conditions known to be unfavorable to mice are winters which are cold and without snow, heavy rains in cold weather, wet springs and very hot or dry summers (unpublished).

After a detailed study of the two, Johnson concludes that the forest deer mice, due to their sheltered habitat, are less subject to the unfavorable conditions mentioned than are the prairie deer mice.

b. Rabbits. The work of Hammond (368) on rabbits is of interest in showing that the effect of weather factors on fetal atrophy may really be a factor determining abundance. On the average of all animals examined, only 70 per cent of the eggs shed at oestrus become normal foetuses, the remainder either do not develop or become atrophic. Fertility of higher animals is limited (1) by the number of eggs shed at each heat period, a large factor in the fertility of sheep and wild rabbits, and (2) by the number of eggs shed which develop to normal young, a large factor with the pig and tame rabbit. In the latter the number of eggs shed at the commencement of each pregnancy gradually increases with the rise of temperature from January to April and then decreases again.

The breeding season of the wild rabbit lasts, depending to a certain extent on the weather, from February to September. This season in tame rabbits can be prolonged by controlling the temperature and food. The proportion of atrophic foetuses increases with the number of eggs shed per ovary. The production of a large number of eggs per ovary frequently outstrips the nutrition available for them and leads to atrophy.

c. Horses. There have been no ecological or climatic studies of horses. The occurrence of young may be significant at this point. Horses are not transported as cattle are for fattening. The greatest abundance of young horses in the United States lies in Iowa and adjacent states in a region of abundant pasturage but also in a region similar to the rich soil area of western Russia (290), where they once occurred in a wild state.

d. Cattle. The ancestor of the northern European domestic breeds of cattle was probably *Bos taurus primigenius*, a deciduous forest dweller, feeding on shrubs and herbs (604, 767). There appears to be no doubt that wild cattle of this species ranged throughout the deciduous forest. They probably did not enter the coniferous forest. To what extent they ranged in numbers into the live oak or Mediterranean forest is not clear. The questions of the remains belonging to late glacial periods appear not to be definitely settled.

Davidson (239) has made a study of three beef breeds and three dairy breeds with results differing from those obtained with sheep.

His general methods are similar to those used by Taylor (881, 882). The localities where all the breeds here discussed were developed are mild maritime climates.

The climatic territory within which the wild ox is known to have ranged in recent times may be represented by London and Hereford on the west, Montpellier, France, on the southwest; Edinburg on the

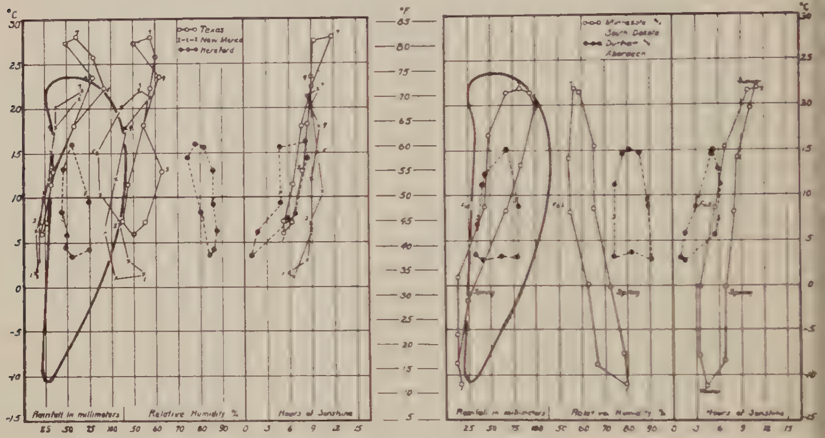


FIG. 19 FIG. 20

FIG. 19. Climatic diagrams of areas occupied by Hereford cattle, by Davidson (239). At the left mean monthly temperatures in °C. is plotted with rainfall in millimeters (hythergraph); in the center, the same temperature data are plotted with per cent of relative humidity (climograph); at the right the temperature data are plotted with mean hours of daily sunshine for the average month (solar graph). The broken lines represent the climates of the places where the breeds originated. The heavy black line shows the limits of mean monthly temperature and humidity in the range of the wild ancestor. The solid lines represent the climate of the "range" areas where cattle of this breed are abundant, New Mexico and West Texas. The range climate is drier, less humid, and more sunny than the place of origin to the extent of being outside the limits of both rainfall and humidity. A minimum of correspondence is shown between two range areas and the ancestral home though the Herefords are the predominent cattle of the region.

FIG. 20. Similar to figure 19. The Shorthorns outnumber the Herefords two to one in North Dakota and Minnesota though the climate would appear equally suitable to both (239).

north, Moscow on the east, and Sophia on the southeast. Only partial consideration was given to a few localities along the Baltic and in the mountains where rainfall is greater in the cool months. Modern breeds have all retained the ability to live in such extremes even though they did not occur in the areas where the breeds developed.

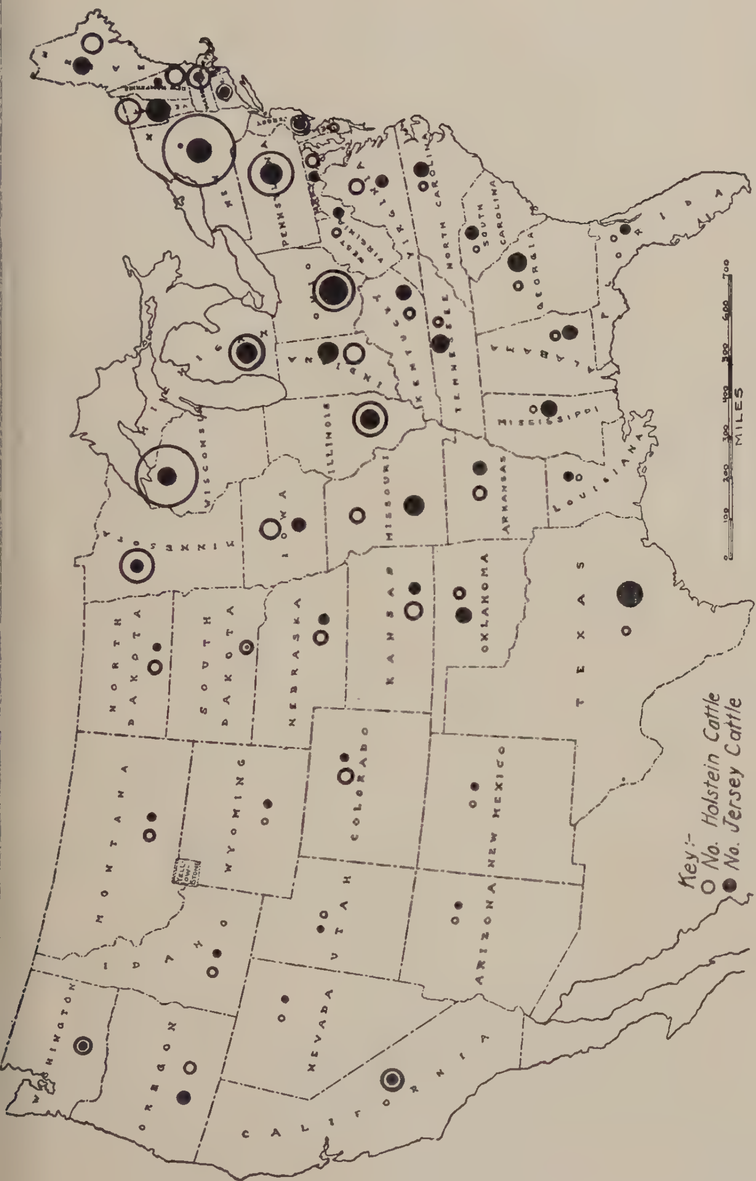


FIG. 21. Numbers and distribution of Holstein and Jersey cattle. The Jersey cattle are much more abundant in the southeastern states than the Holsteins, which are very few in number. The Jerseys predominate as dairy cattle (239).

According to Davidson, the domestic descendents of the wild cow have become inhabitants of arid grass land, subtropical, and semiarid regions. The beef breeds treated (places of origin in parentheses) are the Hereford (Hereford, England), Short Horn (Durham, England) and Angus (Aberdeen, Scotland); the dairy breeds are Jersey (Isle of Jersey), and Holstein (Friesland, Holland).

(a) Beef breeds. Davidson's climatic diagrams of the localities in which these breeds originated shows only small differences between them in temperature, rainfall, humidity, and duration of sunshine, and on the whole considerable difference from the areas where they are not abundant in America. He shows that the presence of abundant pasture and food is essential to Short Horns (239, 297), and Angus. The Herefords are not limited by these conditions but can live on scattered and scanty pasture; the Herefords are suited to dry grass lands and are shown by the reports of the United States Department of Agriculture to predominate in western arid states, while the other two breeds are in moist areas. The toleration of scanty pasture is in accord with the conditions and treatment under which the breed was developed; the climate was a little less arid where the Herefords were developed than where the Short Horns were. The Hereford is then a development of a breed *suited to a type of vegetation*. The type of vegetation is correlated with climate. The Short Horns and Angus predominate where there is an abundance of *rich moist pasture*. The controlling characters of the Herefords are not those of the climate of the home of the breed but rather are the result of the method of selection.

(b) Dairy breeds. The dairy breeds originated in very similar climates adjacent to the English Channel and North Sea. In the United States the Holsteins and Jerseys are predominant in the north and west, while in the southeast the Jerseys alone predominate as dairy cattle.

The Holsteins are restricted to climatic conditions similar to those in which they originated, and with ranges in temperature tolerated by the wild species. Davidson (239) states that the presence of the high temperatures combined with high humidities during the summer months probably limits the distribution of the Holsteins to the north.

High butter fat record Holstein cattle are in northern and Pacific Coast states where the majority of cattle of this breed are located.

In the case of the Jerseys there are two-thirds as many purebred cattle in the southeastern states as in the northern but only one-sixth as many high fat producing cattle.

4. Birds

The domestic hen is better known in this respect than any other bird. Assuming that *Gallus bankiva* (98) is the principal ancestor of the domestic hen, we find that the wild fowls breed from March to July in the Himalayas and earlier farther south and lower down,

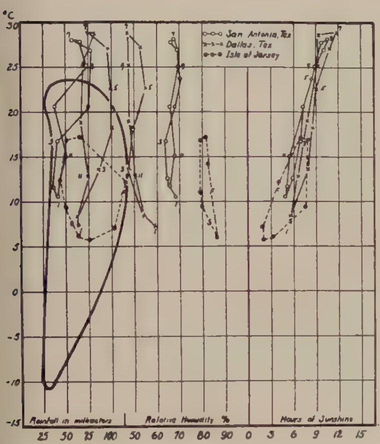


FIG. 22

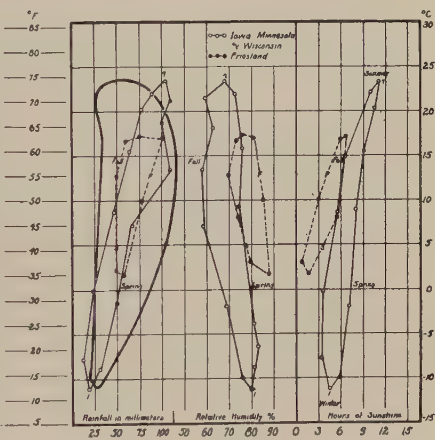


FIG. 23

FIG. 22. Climatic diagrams showing that the temperatures tolerated by the Jerseys in the southeastern states are in excess of those of the original habitat or herd home (239).

FIG. 23. Showing that the Holsteins are limited to climates similar to those of the original home and habitat (239).

and just before the beginning of the rainy season. Steggerda, using the same methods (1009), has shown that the areas of greatest numbers of hens, e.g., Petaluma, California, are dry and warm in the months in which hens normally lay. Localities with cold wet winters and wet springs have few hens. The greatest numbers of hens are in the localities with warm dry spring months. Neither temperature nor rainfall considered alone is a necessarily limiting factor in the distribution of poultry, but when both cold and wet conditions prevail poultry do not thrive. If other environmental conditions are equal, we would conclude that domestic poultry

thrive best under climatic conditions where the breeding season of the domestic breeds approaches that of the wild ancestors.

5. Insects

Several important facts have been brought out by the use of climatic diagrams (294, 820, 826, 924) in the study of the relations of insects to weather and climate; several of these contributions have not been carried far enough to make safe correlations and have failed, probably from insufficient analysis or insufficient knowledge of the variations in the condition of the population of the species. It is necessary to do more than make a few diagrams.

Cook's (201, 202–204, 207) work on the pale western cutworm has been productive of good results in the matter of prediction. Cook introduced a line passing through the axis of the climograph of the optimal climate which served to orient the figures for less favorable climates. The present writer (826) discovered and predicted the type of year favorable to the codling moth and likely to cause it to seriously damage the apple crop, by means of such diagrams. A line with arrows showing the seasonal trend was added as passing through the centers of the monthly limit determined by Johnson's method (see fig. 62, p. 159). The following citations have to do with the use of such diagrams in the study of insects: (340, 294).

V. PROBLEMS OF PARTICULAR CLIMATES (389, 932, 933, 944, 945).

As a rough general guide to the consideration of different climates, it may be said that a factor is most important where there is least of it; rainfall and its variations are most important in the desert; length of summer or unusually high temperatures in the tundra; dry periods in regions of uniformly distributed rainfall. It is not necessary to discuss all climates; the general principles may be illustrated by the desert on the one hand and the rain forest on the other.

1. Desert (139, 140, 418, 847)

Seasonal distribution and distribution through succeeding years are most important facts concerning rainfall. For both temperature and relative humidity, great daily range and extremes are significant. Strong winds and high evaporation add to the hostility of the climate. Maximum and minimum figures show best the difficulties of desert life, since deviations from the mean are so great and common.

Soils of the desert have their special problems. Sand is hard to colonize but holds water at a depth. Clay and silt have high evaporation and salt deposits. Gravel has poor flora. Water courses show relatively rich life, which is subject to frequent destruction. The floral environment is of three kinds: annuals growing only after rains, perennials with underground parts perennial, and perennials active throughout the year.

Many animals have a life-history fitted to the period of growth of annuals. Adaptations appear in aestivation and storage for dry season. Water-supplies besides rain include dew, water contained in plants, water-holes, etc. Devices to escape the intense sun of mid-day include use of burrows, caves, bushes, and small stones as shelter.

Sumner (870, 871) has pointed out numerous relations of mammals to climate and correlated conditions in arid regions. He states that desert mammals are probably not exceptionally well adapted to enduring high temperatures. Some desert rodents are known to succumb to a comparatively brief exposure to temperatures which are not harmful to man. Burrowing mammals are mainly nocturnal, and remain underground during the day time, at depths where the temperature is much lower than that of the air. Desert rodents only occasionally have access to free water, except such as is contained in succulent plants. These are probably freely eaten by most species, and are essential to their health. Kangaroo rats and pocket-mice appear to be least dependent upon free water, and have been known to maintain themselves for long periods upon a diet of air-dried seeds. In respect to their water requirements, Sumner further states that it seems unlikely that desert rodents differ materially from their nearest relatives in non-desert areas. The latter may also obtain sufficient water from succulent plants, and in some cases may live indefinitely upon dry seeds. In general Sumner believes that there is no reason why the persistent scarcity of food and water should result in a peculiarly savage struggle for existence in deserts. It is likely, however, that the periodicity in the food and water supply may lead to exceptionally great fluctuations in the pressure of population upon subsistence. A rodent population, engendered during the period of relatively abundant food supply in the spring and early summer, may normally face famine some months later, and thereby be greatly reduced in numbers. The special need for spine protec-

tion among plants in arid regions may be the result of the recurrent intense pressure of population upon subsistence just referred to. Most desert mammals belong to families and genera which range widely into non-desert areas. Sumner states that in many cases they are only subspecifically distinct from forms which are abundant in regions of high humidity. The great majority of our desert mammals show no obvious modifications of structure whatever. In even the most thoroughly xerophilous group among them, Sumner finds it difficult to recognize any of their structural peculiarities as special adaptations to conditions of extreme aridity.

2. Rain forest

The tropical rain forest of Barro Colorado Island will serve to illustrate the type of relatively uniform climate with its dense vegetation. Allee (15, 16), (1926) has summarized conditions and animals essentially as follows:

(a) In the whole Canal Zone there is little change in barometric pressure from one year's end to another. In the rain-forest, the total variation for a week amounted to 0.17 of an inch, only.

(b) In the rain-forest the horizontal air movement is practically nil near the forest floor. There is a marked gradient in air movement between the floor and the canopy, and a still more marked one from a partially protected position in the forest crown into the free moving air overhead.

(c) The temperature near the forest floor out of sun flecks is remarkably constant, much more so than in the tree-tops where the temperature mounts rapidly in the sunshine. The temperature conditions in the forest canopy resemble those of the open spaces.

(d) The evaporating power of the air on the forest floor, even during the dry season, shows approximately half the evaporation rate given by an instrument in the forest roof protected from wind and sun or by one placed in a partial clearing. The evaporation over the neighboring lake is approximately three times that of the upper forest and almost six times that of the forest floor.

(e) The measurements of light intensity give quantitative data concerning vertical and horizontal light gradients in the rain-forest and demonstrate that the illumination of the forest floor, as with all factors measured, shows relatively little variation either from day to day, or between day and night. The vertical gradient for the dry season shows the forest canopy to have an average light intensity of 25 times, and above the forest roof 442 times, that in the shade on the ground. Similar differences exist between the denser forest and large sun flecks or open, unshaded situations.

Visher (933) has pointed out the usually unnoticed and unexpected features of tropical climate. There are many important local studies

of climate. Weese (960) has studied deciduous forest conditions and compared results with Lorenz-Liburnau (535). Clements (174, 175) in "Plant Indicators" (176) and in many other publications, discusses climate in central and western United States from an ecological viewpoint. Pearson (660, 661, 662) has studied conditions in Arizona and New Mexico. Much information has been gathered by Shreve (839–841).

Numerous treatments of climate based on temperature and rainfall, etc., are available—Koppen's (944), Herbertson's (389), Parkin's (651) temperature map, and others. These serve a good purpose in interpreting the climate of various regions, and the rather close correspondence between the region and natural vegetation speaks well for both the idea of organisms as indicators and for the physical criteria applied.

The purpose of this chapter is only to indicate some of the problems of climatology and ecology. The succeeding chapters are devoted to the analysis of climate by additional field methods and by laboratory methods.

CHAPTER II

Methods and Results of Biotic Observation and Experimentation

I. INTRODUCTION

Modern ecology has for its fundamental aim the interpretation of communities and the relations of particular organisms in communities. The causes of fluctuations of populations of species are important, both physiologically and biotically, and are traceable to variations in conditions. In the case of the more important and controlling species the causes are probably physiological. Accurate methods of quantitative observation and biotic experimentation are essential to an unraveling of the controlling factors to a point where laboratory methods may be used. Finally the combined field, garden and laboratory methods must be used together.

II. BIOTIC AND CLIMATIC OBSERVATION

A. General working hypothesis

Modern field ecology has added to our working knowledge largely through the evaluation of the relative importance of different organisms. Those who are unfamiliar with these methods and principles have been of the opinion that progress cannot be made by such means as are advocated in this chapter. The recent work of Transeau (908) in correlating the destructiveness of the corn borer with biotic communities in Ohio and in Europe has served to overcome some of this prejudice.

It may be assumed as a working basis that each community includes certain predominants (26–32, 33, 62, 64, 72, 73, 87, 97, 248, 258, 269, 369, 379, 427, 442, 476, 563, 580, 744, 751, 752, 760, 802, 804–7, 809, 823, 840, 849, 889, 890, 907, 930, 931, 938, 947) and also less influent animals which are nearly always present in any year and are physiologically adjusted to the average climate of the region and to a certain stage in succession. The predominants are selected on the basis of size, weight, abundance, and influence. This is true of the selection of dominant trees in a forest as compared with shrubs,

herbs, ferns, mosses, and lichens. Among animals differences in size are important; the larger mammals, however, rarely rival the trees in either numbers or importance. The true predominants may be found exerting important influence on the community at all sea-

FIG. 24. Some predominants of a marine bottom community in the Thisted Broad (Echinochardium-Cyprinia formation), eaten by plaice. The numbers shown are those occurring in the random samples of 1911–1914, on one-fifth square meter. It shows marked fluctuation of some of the predominants (from Jensen, (438)).

sons. The sub-influents are inconspicuous and non-important in some seasons and numerous in others; some of these do not fluctuate greatly from year to year, others fluctuate greatly.

For experimental study of relations to average conditions the more

stable ones should be chosen while the fluctuating species serve to determine the effect of variable and rhythmic factors.

From the point of view of indicators (179), the selection of species for experimental ecological and climatological study in and outside

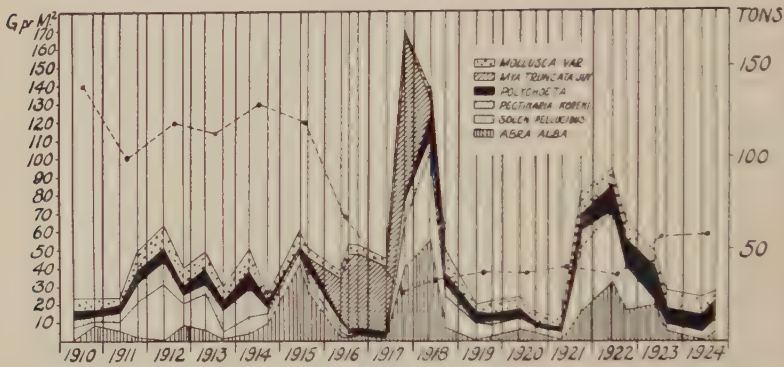


FIG. 25. Showing the fluctuation of fish food in Thisted Broad 1910 to 1924, in grams per m². The broken line shows the yield of fish (plaice) in the same years (from Blegvad (101)).

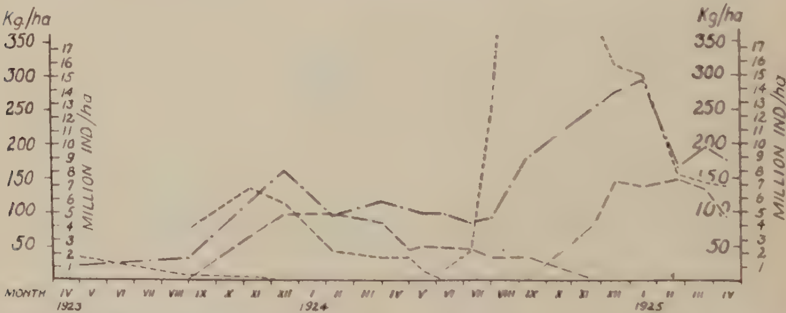


FIG. 26. Showing variation in the number and weight of the larvae of Chironomus from month to month, April, 1923, through April, 1925, in Platten Lake (Plöner Becken). The short dashes are for the numbers of Bathophilus larvae; the long dashes are for the number of Plumulosus larvae. The dot-dash line is for the total weight of larvae of both species. This is the average for the whole lake for the second year and all but the zone 0 to 4 meters for the first. (from Lundbeck (540)).

the laboratory is very important. In climatic work, the species should never be selected at random, without reference to its biotic significance. The purpose of field observation is first to afford a

basis for the selection of species suitable for study as *general indicators* of biotic and climatic conditions. This is determined by abundance over a geographic range and in good and bad years (101, 438) (figs. 24, 25, 26). Secondly, field work must determine the abundance and success of various species studied experimentally.

Certain perennial species of animals are of interest because of their influence on the biotic community, and the very abundant species because they are presumably best adjusted to the climate and other conditions and hence the best indicators of climate, etc.

B. Census methods on land (53, 155, 233, 587, 795, 894, 895)

The determination of the most abundant and important animals involves general quantitative methods on land. Quantitative studies on land usually include *cruising* or *observation* and various methods of trapping, random sampling (358) and enclosure for counting on definite areas. (See 1001–1005.)

1. Cruising. Cruising is necessary to determine the number of large animals such as birds, mammals, and even reptiles but the principle may well be extended to observation and counting of various small forms on a unit area (155, 311).

Cruising has been practiced for deer and other large game in some of the game preserves where cattle are grazed, with cattle used as a check. A ranger counted the number of deer and the number of cattle seen from horseback in riding a given area. The total number of cattle being known, the number of deer was checked and corrected accordingly. Cruising for large game has commonly been done from horseback. In the case of deer valuable information can be secured by counting freshly shed antlers after the shedding season is over.

The determination of predominants, fluctuations in population, etc., demand quantitative methods of all kinds designed to determine population as concerns each important species either resident or visitor. It is obvious that continuity of observation is essential.

Small mammals with nests or burrows may be estimated by counting nests and colonies and multiplying by the number in the average colony. Tracks may also be utilized.

Nesting birds are difficult to estimate, though the number of singing males at nesting time gives a good basis, or nests are easily found. Forbes (307) and Forbes and Gross (311) made an important contribution to the study of the abundance of birds by cruising across

fields and through wood lands. There are no essential difficulties in cruising for amphibia and reptiles, or even certain invertebrates.

Observation of insects is also necessary. In this case it consists in observing a tenth square meter until the small animals have been noted and their activities recorded, and numbers estimated.

Driving is sometimes practiced especially for scattered animals such as coyotes or wolves. A large number of men with dogs and much noise scare and drive the game toward a center agreed upon.

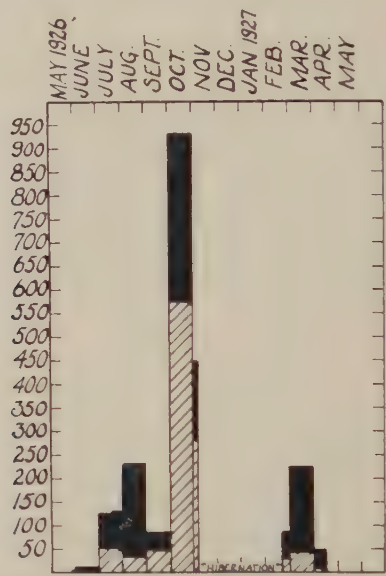


FIG. 27. Showing the number of cluster flies taken in traps for the various months of 1926-27 at Urbana, Ill. The solid black is for females and the oblique lines for males. The importance of trapping for seasonal abundance indications, is suggested. (from Decoursey (244)).

Such drives secured four coyotes in Champaign County, Illinois, in 1920, from approximately 70 sq. mi.

2. *Trapping.* Trapping may be carried on with reference to all kinds of small animals, insects, birds, mammals, reptiles and amphibia. All kinds of signs, such as tracks (127), tooth and beak marks, exuvia, hair, feathers, etc., must be taken advantage of in placing traps for individuals. In other words, the investigator must know his animals thoroughly to be an expert trapper and to make his work of highest order from a quantitative viewpoint.

When single traps for individuals are used, Grinnell's "trap day" unit may be utilized. This is one trap for one day set by a skilled trapper. The number of traps should be large and the trapping carried over a period long enough to eliminate the effect of minor fluctuations in weather conditions. Mass traps are frequently used especially for insects and either baited with food or breeding materials, or supplied with a light. Such traps for insects and other small animals are especially useful in determining seasonal abundance of particular species and many other features of aspection (see fig. 27). The value of insect-trapping results is lessened in complex seral stages, due to flight which may bring together animals from several communities, but in larger climax or subclimax areas, the catches represent the population of the area.

When comparisons are made between different habitats, the trapping should be carried on simultaneously in the different habitats and where areas are some distance apart the trapping should be carried on in the same season and every precaution taken to check and determine weather effects.

(a) Trapping for land vertebrates. Traps which capture the animals alive are desirable wherever it is possible to use them. Box traps and snares are valuable. For mice, there are numerous live traps of both wire and wood. Burt (138) has described a simple trap made from a guillotine trap and a small tin can. The U-lever, which usually crushes the mouse bears a piece of screen and stops in a vertical position, closing the can.

Traps which kill should not crush the skull and should be small and light enough so that they can be carried into the field and set in small spaces. Of the traps for small mammals, those that catch them by the shoulders are most practical. The "It" trap is an example.

Several kinds of traps have been made for catching small grain-eating birds and have been used especially in banding work. Descriptions are included by Lincoln (518) in his instructions for banding birds. Methods of catching birds are fully illustrated by Nelson (622).

Traps for reptiles and amphibia must be devised in accord with their habits. Some amphibia traps have been made by placing tiles in the ground to make pitfalls with adjacent screen leads to direct the animals to the pit.

(b) Trapping for terrestrial arthropods. Entomologists in their work against specific pests have developed such things as poisoned baits (as for grasshoppers, cutworms, etc.); barriers with trap pits (grasshoppers, cutworms, chinch bugs, etc.); hopperdozers and hoppercatchers (grasshoppers, etc.); sticky shields (leafhoppers, etc.). These methods, though useful in control work, are not necessarily so in quantitative work or for the determination of the character of animal population of a locality.

Traps of various kinds have been used; these fall into the following groups: (1) mechanical, (2) baited, and (3) light traps. Mechanical traps have been used for flies, mosquitoes (295). They may be used with proper precaution to determine seasonal variations in abundance. Baited traps are used for cockroaches (950), for various Diptera (648, 795, 796, 949), for moths, (289, 867), etc. These usually have poison added to the attractive substance. Traps of this nature are likely to be selective, catching only certain forms. If the bait could be made up the same every time, seasonal variation of attracted forms could be studied. Baits are not likely to be uniformly effective under all weather conditions. Wind causes odor to spread in only one direction, moisture weakens the bait unless it is covered and lack of moisture dries the bait, thus reducing its effectiveness.

Collectors have recognized the attractive power of light as shown by the clouds of insects frequently found under and around street lights, and light traps have been devised. The light has often been in the form of gasoline lamps (528, 768). In some there is a reflector behind the lamp (911, 912); this type is undesirable since insects come to the light from in front of the lamp only. The better traps have their lights so fixed that insects are equally attracted from all directions (76, 485, 528, 768, 912, 975). It is frequently found that male moths are predominant in the catches at light traps, (76, 768, 912, 975) and the females decidedly fewer.

Light traps are probably the most useful type of trap, because a light is easier to maintain at a set standard than is bait; its attractive power is effective to a greater variety of insects (199, 205, 207). Light is not affected by weather conditions as is a bait.

Banding of trees with some sticky substance, as in gypsy moth and brown-tail moth control, may prove useful in determining population of forest trees, with especial reference to the trunk crawlers (133, 134, 337, 416).

Breeding of parasites from plants and animals, especially other insects (528, cages for examination), and caging sample populations are important and may be carried on in darkness with tubes or bottles projecting into the light. Most insects will enter into the tubes which may be removed from the outside. This method may be extended to cover operations similar to the cylinder method described below.

The stomach contents of mammals, birds, reptiles, etc., will often contain the predominant species as well as the rarer ones which might be overlooked.

Yaghi (992) used the Roentgen ray to detect boring forms. This method might not be practical for use in the field.

3. Cylinder method. A cylinder with closed top is p'aced over an area, pushed into the ground (475, 769, 984). A volatile poison which acts as a repellent should first be poured in a ring about the cylinder (K. M. King, personal communication) and then introduced through a small opening at the top. After all animals are dead or anaesthetized they are removed and counted. On land, cylinders 25.2 cm. in diameter covering 0.1 m^2 to 54.3 cm. in diameter covering 0.25 m^2 may be used. Such cylinders must be provided with a stiff sharp edge. The cylinder must be placed at the hour of minimum temperature to prevent the escape of active insects. King (personal communication) used a heavy sharp ring of the exact size of the can, to drive into the soil so that the soil collection may cover the same area as the can. The ring projects above the ground 3 cm. and below 7 cm. Either with or without the ring a sharp knife must be run around the can to cut away the vegetation and seat the edge in the soil. Whether soil animals are to be included or not, it is necessary not only to remove all animals that may be seen, and all the vegetation for examination, but it is also necessary to remove all of the surface of the soil. This is essential to get all the animals that are above the soil and that fall out of the vegetation. It is necessary to split all plant stems of any size and inspect for insect borers, etc.

Many arthropods can be recovered by placing the soil in water; the air in the tracheae of most arthropods causes them to float. This is not true of delicate winged insects such as Diptera. In these cases the wings become entangled and the body does not float. Where these are present it is necessary either to hand-pick the surface

material or anaesthetize the animals without killing them and then put them into one of the hot water funnels or similar devices described below. Soil washers and some means of keeping the different depths separate must be provided (1010).

4. Soil washers and other devices. The soil washer (fig. 28, *C*.) of Morris (603) has been used to a considerable extent for removing insects from soil. Some such method is of necessity employed or the work of looking over the soil is inaccurate and becomes prohibitive because of time consumed. The Berlese funnel (79), which is a large water-jacketed funnel similar to those sold by apparatus houses, but about three times as large, may be used where

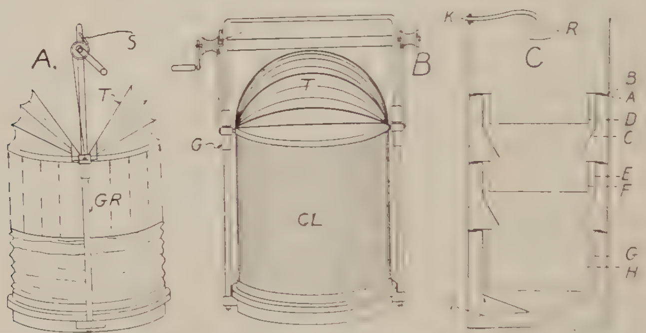


FIG. 28. Land collecting equipment. *A*, insect trap closing; *B*, closed; *C*, soil washer of Morris (from (603)). Median vertical section of soil washing apparatus: *a*, ledge; *b*, shelf; *c*, first funnel; *d*, first sieve, with holes 3.5 mm. in diameter; *e*, second funnel, *f*, second sieve, with holes 1.5 mm. in diameter; *g*, third funnel, *h*, third sieve, with 50 meshes to the inch; *i*, outlet for water; *k*, pipe connected to water supply; *r*, rose or shower nozzle.

there is much débris. Débris may be placed in a container with coarse screen bottom immediately above the mouth of the funnel; as the small animals are heated by the heating of the water in the funnel they fall through the screen and slip down the funnel and into a bottle of alcohol.

If discretion is used in placing the cylinder, and care is used in securing the animals, this method may be quite accurate. The cylinder method is the final criterion of abundance of small animals. The general plan, however, needs expansion. An apparatus being tested at present consists of a narrow ring 5 cm. wide and 57 cm. in diameter to be placed on the ground or held on a tree trunk and a tight cloth cylinder of the same size 60 cm. high carrying a ring at the

top with a four-bowed hemispherical top closing at the center (fig. 28, *A*, *B*). The apparatus is placed in position with the cylinder collapsed to the ring and the top open; the cloth parts rest on the ground and only two vertical guide rods project upward. Time is allowed for all animals to assume a normal position, when a spring is released by a person some distance away, which draws the cloth cylinder up, and the impact against the top of the guide rods releases a second spring which closes the top. All the animals above the soil are thus quickly trapped and may be anaesthetized and removed. By fastening the apparatus to a bottom made in two halves to fit around a branch or small tree trunk, similar collections may be made from these positions. A curtain roller is best for the spring.

5. Netting. The sweepnet is a useful instrument but must be standardized by means of cylinder and other methods. Weese and others (769, 797, 851, 960) made sweepnet collections at the time of making cylinder collections. King (personal communication) at the beginning of his studies swept at the time of maximum activity but later did so at both times. The size of the net, height of the vegetation, length and frequency of strokes, the temperature, light, wind and moisture are all factors influencing the efficiency of the collecting from a quantitative viewpoint.

In the use of the sweepnet the height of the vegetation is an important factor. If several people go over an over-grazed or short grass area with a sweepnet the difference in number of animals secured will vary enormously, due to the difference in the height at which the net is used.

Again, when the temperature is high the quickened activity of insects also modifies the results—tends to cause some to escape. Here some form of trap that can be sprung from a distance is desirable. This field presents difficulties but the error as regards small animals may be checked, whereas in water the error is less easy to ascertain and so goes unnoticed.

If the sweep net collections are representative, and can be evaluated into terms of numbers per unit area, it does not matter what the method of using the net may have been. However, some form of standardization is desirable. King has further stated that under certain temperature conditions occurring in the spring and autumn the net and cylinder collections are in agreement. His method of sweeping was designed to take a stroke 1.5 meters in

length with a 35 cm. American folding net at such intervals as would make each stroke the first disturbance of the vegetation covered. He

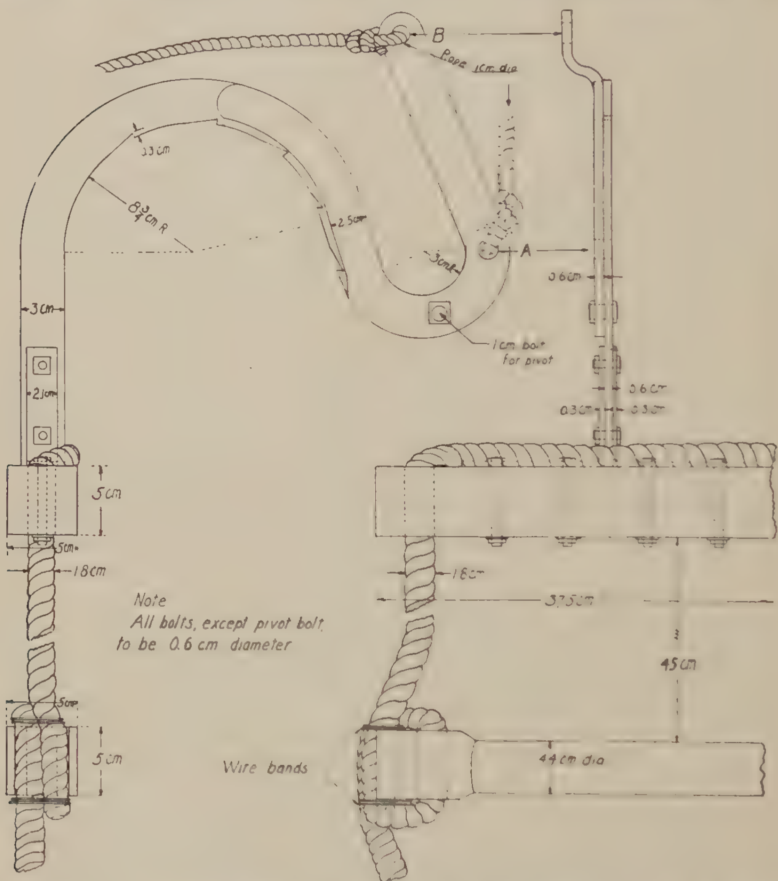


FIG. 29. A portable ladder designed by F. A. Davidson for use in getting into the crowns of large forest trees. A release lever has been added. A 600-gram weight is thrown over a limb 6 to 12 meters from the ground, while tied to the hole *A* by a hard cotton rope, 20 meters in length. The hook is drawn over a limb and the ladder utilized. Before leaving the tree the investigator ties the rope in hole *B* and throws the rope over a limb higher up and behind the ladder. A pull at hole *B* releases the teeth and the ladder is lifted and lowered by the cotton rope.

took the height of the vegetation into account and corrected for it. He advocates the standardization of the methods along these two

lines. He made collections with strokes in one direction with the same distance between strokes. There is, furthermore, no doubt that the standardization should consider operation with the net in tree tops and the branches of low trees too large for this usual sweeping.

The use of the sweepnet without careful observation of the vegetation at the time of sweeping is always open to the criticism that the animals were not all high enough in the vegetation to be secured, and especially that they move up and down with the physical conditions, and so the number taken in the net may vary from hour to hour. This is one reason why the use of the net is an inaccurate method.

It is possible that the use of some modification of Domralscheff's (254) quantitative dredge, provided it could be so constructed as to cut the vegetation, might be practicable but it has not been developed.

For work in trees a few investigators have used platforms and fixed ladders at permanent stations. Davidson designed a portable ladder shown in figure 29. By throwing a weight over a limb and drawing the hook upward it is caused to drop over a large branch. It can be successfully placed 12 to 15 meters from the ground, thus facilitating the examination of the bark on the limbs and the use of the net among the leaves.

C. *Census methods in water* (*395*)

1. Plankton. (84, 85, 454, 455, 462, 486, 487, 575, 612, 619, 697, 860, 863). Much more quantitative work has been done in water than on land. Such study of plankton is quite logical and easy and because of its supposed importance has been carried on as economic work relative to fisheries. Some good work has been done—the predominant organisms are known and considerable is known of the seasonal societies in a few localities. There have been but few attempts to organize the data about communities into a scientific order. Most of the work lacks continuity, but the predominant and permanent organisms of the plankton of some parts of the sea and certain fresh-waters have been ascertained for some seasons. Various quantitative methods have been followed. The student of ecology will find little difficulty in selecting plankton organisms which will show responses to the large rhythms of conditions or which fluctuate widely with minor variations in conditions from year to year or month to month. Allen and others (26–32) have made daily collections from

the pier of the Scripps Institution with the result that the necessity for continuous observation is emphasized, the importance of life history studies strengthened and ideas of single controlling factors ruled out. Birge and Juday (91, 616) have also maintained continuity in their observations on Lake Mendota, with similar general results.

2. Bottom Communities. Quantitative study of bottom life has been carried on by various means. One of the simplest and most effective is the cylinder method, in which an open-topped cylinder is placed in water from 1 to 2 meters deep, pushed into the mud and all organisms removed. This method has the advantage of securing the slow-moving animals and the plankton; when manipulated with discretion it is the best of quantitative methods. The same principle carried on with nets of large size and depth and "pull in" bottom may be used for fishes.

All manner of "quantitative" bottom collecting equipment has been used. Thienemann (890), Reighard (943), Petersen (670), Behning (69a) and Domralscheff (254). The implements include all sorts of tubes, cylinders, bottom scrapers and grabbers, and the common naturalist's dredge which is least effective quantitatively (478, 484a, 670).

The writer's experience with these is limited to the Petersen bottom sampler, both *soft* and *hard* bottom types, both of which are effective, and the Ekman sampler. The first when closed is a cylinder in horizontal position, and is effective on both soft and hard bottom. It has been used for all kinds of bottom in fresh water. The hard bottom sampler is fairly effective even on rock (Kirsop (478)) where its efficiency can be tested in shallow water where observation is possible. The Ekman dredges which the author has utilized have been essentially useless in streams as grit prevented the closing of the jaws.

The writer has found a small triangular dredge with 30 cm. sides and three slender rods, one from each corner, coming together as a cone 70 cm. in front of the dredge, very effective for use in streams. The edges of the dredge triangle were pitched so as to pull into the bottom. The dredge was thrown from the shore or *shallow* water and pulled in by means of a rope. It is possible to measure the distance over which the net is pulled and make the results quantitative.

Needham (620) has discussed quantitative methods for rapid

streams; his principal contributions are a hand screen to be held below stones lifted from the water, and a screen cone to wash them in.

With the exception of the classical work of Petersen and Jensen (671) (see 669), of Jensen (438), fig. 24, of Blegvad (101), fig. 25, showing large variation of the bottom fauna from year to year, (and the excellent beginning of Lundbeck (540) in fresh water, fig. 26), the studies of bottom communities have too often been without organization or continuity as to sequence, or proper evaluation as to abundance and predominance. In the main the observations have not been carried on from month to month and year to year, which is the first requisite. Such observation must be accompanied by continuous record of hydrographic conditions and by experiments and observations such as were carried on by Blegvad (101).

In the sea and fresh water, in addition to plankton organisms, and nekton and sessile bottom organisms which may be conceived of as comparable to plants on land, there are motile animals some of which swim near the bottom and may be compared to birds and mammals. There are also many slow-going animals large and small which in the sea and in fresh water move about over the bottom and correspond to various motile animals of the land.

These larger motile animals afford most of the difficulties of quantitative work. Cruising is not very practicable in most waters though it should not be neglected. There is no really excellent method of ascertaining the numbers of either purely bottom or purely pelagic fishes. However, the relative number per typical net sample from year to year may be ascertained and will serve as well for many purposes as more accurate information.

D. Examples and results of observations (8, 154, 214, 285, 665, 714, 723–725, 968)

The most painstaking observation of limited areas and the habits of animals is fully as essential in aquatic work as in terrestrial work. The careful work on materials for abodes done by Wesenburg-Lund (968) on aquatic insects is an example. Such observations are important in counting and estimating population.

One of the principal weaknesses of work in census taking is likely to be lack of observation of the forms taken in the random samples. The investigator is likely to have the population data and to have failed to note the food plants, evidences of biotic interaction, and

minor or seasonal communities. It is important to include such data, for they are of great ecological importance. Their omission prejudices a large class of readers who have too much faith in the current generalities relative to food habits. Every quantitative collection should be followed by enough observation to cover the elementary relations to food-plants, shelter (341, 344) etc., of the more abundant species, in both larval and adult stages.

1. Observations of terrestrial arthropods. The widely known work of the Peckhams and Fabre (285, 662a) on particular species of solitary wasps is to be emulated in the study of the outstanding species of communities. The possibility of far-reaching results is well illustrated by the following extracts from a study by Rau (714).

In speaking of a sheltered clay bank the author says:

> Early in the work it was seen that the many insects did not use the clay bank and the environs in the same way, but they were easily classifiable into four distinct groups.
>
> Group 1. Pioneers. The permanent dwellers in the clay bank and environs, in a general way, the pioneers.
>
> Group 2. Renters. The insects less hardy and more ease-desiring than the pioneers; those which rented or appropriated the abandoned dwellings of the pioneers. They might be called squatters.
>
> Group 3. Visitors. The insects and animals which dropped into the community accidentally, or in quest of shelter or food. They very often influenced the inhabitants, the members of groups 1 and 2, in two ways: by eating them or becoming food for them.
>
> Group 4. Parasites. This contains the names of parasites whose hosts are listed in groups 1 and 2.

The significance of observation in biotic study is well illustrated by the following remarks of the same author:

> To eat and be eaten seems to be the law of the wild. In the interrelation of life in the clay bank, we have repeatedly noticed how one insect falls prey to another. We seldom think of natural death among the insects, but this, too, occurs, and often to a much greater extent than we usually suspect. During this study at the bank, I have often picked up dead and enfeebled insects. Not all the Chalicids fell prey to the spiders and ant lions; I have removed hundreds from the crevices where they had crept in to die. Many mining-bees were picked up dead or limp at the end of their season and many more were pulled out of their burrows. The cuckoo-bees were picked up dead, too—and what enemy could wound a cuckoo-bee in its thick armor? The blister-beetles, *Epicauta marginata*, dropped dead from the plants near the base of the bank. Others found there whose death was not accounted for, were

Iarpalus dichrous Dejean (E. A. Schwarz), *Tachysphex terminatus*, *Trypoxylon* *p.*, *Pseudagenia mellipes*, *Halictus pectinatus*, *Anthophora*, and *Xylocopa* *irginica*. Thousands of dead Chalcid parasites were found in the burrows vhen they were examined during the winter.

One often found newly dead female bees at the foot of the bank. This was ery puzzling, until one day I actually saw where lay the trouble. A returning emale *A. abrupta* found that during her absence another bee of the same pecies had appropriated her nest. A fight ensued, in which the usurper was hrown bodily to the ground and after a few twitches of the legs was dead.)ther fights of a less serious nature were often observed. On one occasion, I aw a female with part of her body protruding from the burrow. I pulled her ut with the forceps, and found her tenaciously clinging with her jaws to a econd female that had evidently intruded in the burrow. The next day also saw the yellow, pollen-laden legs protruding from a bee which seemed to be in gony. I pulled it out with the forceps, and it, too, pugnaciously clung to nother bee, which had evidently taken advantage of the owner's absence to surp her home.

Not all of the soil that came out of the burrows went into the making of the urrets. Much of it was kicked out and fell on the ground below. This was either dust nor pellets, but characteristic minute bits or granules. A very onsiderable heap of these granules had accumulated in front of the center of he bank, where the greatest activity occurred. This strip of drift measured 0 inches in length, 6 inches wide, and from $\frac{1}{2}$ to $2\frac{1}{2}$ inches in depth. This, of ourse, gave the *Tachysphex terminatus* wasps an excellent medium in which to nake their nests, and afforded a material which made pit-making for the ant-ons a pleasure.

It seems superfluous to mention the fact that, had the nature of the soil been ery different from what it was, the colony of insects, especially the principal haracters, the mining-bees, would never have been there, since a firm, clayey oil of this nature is quite essential to masonry of their kind; and too, if these ioneers had not thrown out a large mass of granular soil to the bottom of the ank, there would have been no ant lions, for these never dig pits in firm soil.

E. Importance of aggregations

It has been urged that the common occurrence of aggregations uch as are described by Allee (17–20, 126) may vitiate the results of andom sampling. This criticism comes mainly from those who are vithout experience in random sampling. Predominant animals are ot often in aggregations. Some important predominants occur in olonies, e.g., ants, but one rarely secures a cylinder sample from a olony by accident and corrections are easily made for this when it oes happen. Colonies of many species such as ants, bees, kangaroo ats, prairie dogs, etc., can easily be accounted for. In the sea such ggregations are rare so far as indicated by large numbers of samples.

The marine and fresh water samples show relatively uniform distribution of predominants. It is as it were a duty of the investigator to avoid falling in error of this kind and ordinarily he has no difficulty in doing so.

III. TAGGING, BANDING, AND MARKING

In connection with the studies of life-histories (172), migration, and other activities, the marking of individual animals is necessary. Marking of migratory animals (78, 141) is well illustrated by bird-banding (622) and salmon marking operations (333, 728).

1. Birds (622, 518)

Small aluminium bands supplied by the United States Biological Survey bearing the abbreviation "Biol. Surv. Wash. D. C." and a number, have been placed on the legs of birds trapped for release or on young birds and others affording the opportunity. The number, date, and locality are reported to the Biological Survey at the time of banding and again when the bird is retaken and the band discovered. These bandings have been successful in showing that birds often return to the same nesting place, and to the same winter home. It has also indicated something of migration routes and the age of birds.

Important results have been obtained by Watson and Lashley (951) in carrying birds a distance from their homes and studying their return. They worked on homing of noddy terns and sooty terns of the Tortugas. The life-histories, habits, normal activities, etc., were carefully studied. The birds were marked and taken away to various distances, and nests were watched to note the return of birds. These homing experiments were conducted by releasing birds as far away as Key West, Mobile, and Galveston. In many cases birds did not return, but enough returned to demonstrate "that the noddy and sooty terns can return from distances up to 1000 miles in the absence of all landmarks." No explanation of these remarkable returns could be offered.

Proximate orientation was also studied experimentally in the return of birds to their own nests on Bird Key. Importance of visual and kinesthetic stimuli is emphasized. Orientation in the nest locality gives two points of negative evidence relating to orientation at greater distances:

Birds show no evidence of the possession of special sense of locality, s magnetic sense. There is nothing to suggest birds can retrace ath by memory of successive directions and distances when these ave been experienced only once.

2. *Mammals*

Allen (22) banded bats and found that they return to their roosting laces and remain in the vicinity. M. S. Johnson (452) etherized vhitefooted mice, characteristically marked their ears and turned hem loose at some distance from their nests in a study of homing. They commonly returned home and were retrapped. Beatrice John-on's work (446) carried out on Mount Desert Island mice, also indi-ated the retrapability of mice. She marked a pattern in the ears vith a metal punch used to mark the toes of day-old chickens.

3. *Other forms*

Salmon have been marked young (728) and taken again while n route to their breeding grounds or after their arrival there. Adults ave been tagged and released. The tagging and marking experi-nents though in many cases uncertain in result have shown that the almon return to the stream in which they hatched, and many other mportant facts (333, 346–350).

Marking of insects has been a practice (266, 439, 623), in connec-ion with certain lines of work such as on ants, bees (623) and wasps, n connection with homing, and on various other insects in connection vith pollination studies. The most extended studies have, however, een on the flight of flies, e.g., by Bishopp (94). Bishopp states in a ersonal communication that the best marker is a powdered red halk, a non-oily crayon often sold by art dealers. The general liter-ture and conclusions are summarized by Parker (648) who gives nethods of marking flies and of providing self-marking while feeding. Colored chalk, white enamel, gold enamel have been used with suc-ess. Spraying with rosalic acid on liberation, and an alkaline solu-ion on recovery, or gentian violet and gum tragicanth has been ound useful. Jepson (439) describes additional methods and gives nformation as to durability.

Honey bees have frequently been marked. F. C. Nelson (623) ound that Klondike bronzing liquid made the best marker for rela-ively permanent marking. Of the available colors, extra-fire,

aluminum, gold, orange, apple green, and marine were readily distinguishable. A pointed stick was best for applying the colors. He describes methods of handling bees for marking and suggests chilling at 7°C. as most practical.

IV. SELECTION OF STATIONS FOR OBSERVATION AND COLLECTION

No research operation demands more general knowledge, experience and skill than the selection of stations for study. It is at this point that broad ecological training, especially in the field, is demanded. It is to the lack of such training that many shortcomings are to be laid. This is apparently especially true of investigators of terrestrial animal ecology who usually lack knowledge of physiography and plant ecology with many ill results. This lack while serious is by no means so glaring as is the manner in which plant ecologists with a few noteworthy recent exceptions, have almost completely ignored animals both specifically and generally (210).

The tendency in aquatic work is better and the training of the workers is better due to the influence of quantitative plankton study and bottom sampling. Here it has long been a practice to establish so-called stations and take samples from time to time. These stations have been selected with reference to lack of disturbance of the area, physical factors, etc. Occasionally the selection has been made with reference to communities. This is true of the work of the Danish biological station. In the matter of method of selection and laying out of stations there has been little improvement on the principles laid down by Clements ((173) 1905).

1. *Land stations*

a. Quadrats (173, 209). The quadrat is the usual unit for study and on land the term refers to 1 square meter which is selected as representative of the larger area to be studied. The practice of the plant ecologist is to count and map the individual plants on the area, which usually does not injure them. The quadrat may be staked and examined from time to time over a considerable period, when it is known as a *permanent quadrat*. It is obvious that it is quite impracticable to count all the small animals on a square meter and leave them there to grow or reproduce as the plants do. It has been found quite essential, however, to lay out such permanent quadrats for the observation of animals while animals are removed entirely from other

mall areas. In the employment of the cylinder method the small r minor subquadrats must lie in a larger representative area or ıajor quadrat. The major quadrat should wherever possible be at east ten meters square or 100 m.² in some other form. When the ıajor quadrat is 100 m.² or less, discretion has to be used as to the umber and size of small areas which are to be denuded semi-monthly n the use of cylinders, etc. The major quadrats as well as the minor nes are governed as to size by the size and habits of the species estiıated; half a square kilometer is suitable for birds. Ten square ilometers is probably large enough for deer and comparable animals.

Denuded quadrats are areas from which the vegetation has been noved and are fully as important in animal studies as in plant studies, ut because of the motility of animals 10 m.² areas are quite small nough.

Transects are especially valuable. They are of necessity belt ransects (Clements (173)) i.e., bands 0.5 to 1 meter wide for minor uadrats, and as wide as circumstances permit for major quadrats. These are especially necessary on sloping ground near water. Conour lines should be established in all such situations, as water relaions are very important. This requires the use of a transit. Such ransects may often cross the stream or pond so as to cover different opographic features on the two sides. This is usually convenient in he case of the smaller stream valleys because the steepest and least table (eroding) side of the valley is usually opposite the flattest depositing) side. Longitudinal studies of stream valleys are valuble but they can usually be best carried on by the establishment of najor and minor transects and quadrats at intervals throughout the alley. Reconnaissance methods should be applied in the intervals etween the transects.

2. Selection of aquatic stations

The same general principles hold good in the case of aquatic abitats or on land. Quadrats are less often feasible and transects he commonest type of station in work on streams and small bodies f water. On depositing sea shores such as clam beds the use of a ransit to establish contours and the fixation of a definite starting evel are imperative; otherwise different beaches can not be compared.

In the larger bodies of water, it is necessary to locate stations by neans of the compass or by land marks on shore. Some navigators

are very skillful in the former method and the biologist has no difficulty in acquiring skill in the latter method.

Longitudinal studies of small streams are important especially for demonstrating close dependence upon conditions. These are commonly carried on by means of stations at intervals and reconnaissance between. The method of physiographic analysis demonstrated by the writer (807) brings out the relation of smaller and larger streams both from the standpoint of life and of physiography. In this connection, it is important to determine the average slope of the stream stations and elevations above some fixed point.

Denuded quadrats of the usual type are practicable only in the intertidal belt of the sea and in very shallow water. Pierron and Huang (677) placed terrestrial rocks in the intertidal belt. A personal communication from W. E. Allen indicates that the planting of wood or other materials is being started at his institution.

V. TAXONOMIC IDENTIFICATION

The more abundant and important species must be identified in a manner that can leave no doubt as to what species is involved. Samples of all material collected must be preserved. Adequate space must be available for storage and care of such specimens in connection with every continuous project. This gives a new function to the modern museum which is so important that Ruthven (762, 763) has advocated the conducting of experimental and modern observational work as a part of the regular functions of museums.

In an ordinary study of a terrestrial community the number of animal species represented by one or two individuals per year is very large. One of the outstanding differences between a zoölogical survey and a study of an animal community, lies in the fact that rarer occurrences are usually of zoölogical interest, while the common and abundant occurrences are of primary ecological interest. This means that the interest of specialists in particular groups and of ecologists do not ordinarily conflict to any great degree.

Specialists must ordinarily pass upon the identifications of the predominants, dominants, influents, subinfluents, and other species occurring in sufficient numbers to give the investigator the impression of their importance. In return for this verification of the common species, the specialist should be able to examine and retain if desired, representatives of the rarer species.

The investigator must familiarize himself with the taxonomic characters and specific names of all the species occurring in any abundance. This is an imperative prerequisite to intelligent observation of the habits and activities of the species, and to the identification of such as may enter into the food of other animals. Knowing the insects on the plants at a given time makes possible the quasi-identification of the food taken by birds and other animals feeding during the day. Neglect of observation and the accumulation of large collections of animals unsorted and unidentified is one of the common errors of beginning investigators. This tendency interferes with the proper coöperation of the ecologist and taxonomic specialist. Investigators who fall into this error are more than likely to send the same species to the specialist in quantity and repeatedly, thus consuming his time and lessening his desire for coöperation.

In spite of the frequent unimportance of animals occurring only rarely or occasionally in a community, it is sometimes true that animals showing this type of occurrence at one period may spring into outstanding prominence under suitable weather conditions or at a certain phase of the cyclic rhythm of climate. This makes necessary the careful preservation of all species occurring when identification and recording are not practicable over a considerable period at least. The difficulties in that regard are increased in areas where agriculture has destroyed all but small areas of the original communities. Under these conditions migration into these areas from the agricultural lands increases the number of incidental species. The same is true of small areas of various serial stages under conditions of diversified topography (769). The last two conditions still further emphasize the importance of observation and a thorough familiarity with the species taken in various random samples.

The handling of large series of samples renders impossible the careful methods commonly employed and desired by museum men and private collectors. It is often necessary to inform these men, who are as a rule the specialists one must consult, of the difficulties of the methods employed and of the fact that quantitative collecting methods often damage the specimens obtained, to a degree which makes identification more than normally difficult. Netting and trapping often damage soft-bodied animals and injure the delicate wings and pilosity of certain insects.

1. Care of collections

There are many works on the care and preservation of specimens. The advice given is usually good but too detailed and elaborate for use in quantitative work. The references cited by number cover the field for terrestrial animals as follows: General (570), vertebrates (127, 135, 548), insects (56, 198).

Even for those who have a thorough knowledge of the collection and preservation of all kinds of specimens, short cuts are necessary. This is especially true of the insect group. Here and probably in general the animals in the collections should be divided into two or three classes. In the case of terrestrial sampling, including land arthropods, mollusks, and earthworms, the collections may be divided into two classes: (1) Those insects which must be pinned and which will suffer from going into alcohol, and (2) those which must go into alcohol and probably will not be injured by it. The group to be pinned may be placed between layers of tailor's cotton placed in small pasteboard prescription boxes. The insects requiring this treatment are Lepidoptera, Diptera, and other forms with delicate wings and body pilosity. They may be relaxed later and pinned.

Small animals may be placed directly into 80 per cent alcohol. Within three hours bottles containing larvae should be set in a dish of hot water, with the stoppers removed and left for twenty minutes or more at a temperature just below the boiling point of the alcohol. The heat prevents the darkening and disintegration of larvae, etc., due to lack of penetration of the alcohol. The certain specimens thus preserved in alcohol may be pinned when desirable, at a later date.

VI. BIOTIC EXPERIMENTS AND BIOMETERS ON LAND (179, 675)

In the last quarter-century field experiments in natural communities involving animals have been introduced into ecological procedure. Field experiments are biotic-climatic, in which the whole community is disturbed or partially controlled by exclusion or inclusion of organisms. Quantitative field observations are generally necessary (a) for the selection of the predominants or dominants to be studied as the best representatives of important communities; (b) to determine abundance under *actual* climate either as an independent investigation or as a check on conditions shown to be favorable

in experimental cultures. Rate of development, survival, activity, migration, and general habits can never be neglected in any investigation of this nature. Observations of the Fabre type are also indispensable (285, 714).

1. Civilization experiments

The operations of man in clearing away the vegetation by burning and otherwise, plowing up the soil and excavating, grading and filling are all of the nature of biotic experiments. Plant ecologists have taken advantage of these experiments to a considerable extent, at least enough to secure much information relative to biotic law, especially regarding succession. Animal ecologists and zoölogists have been very slow to take advantage of these opportunities for critical study. They have, however, had their attention focused on the subject by *over grazing* in the western United States, which has shown the small mammals to be of great biotic significance especially in correlation with weather factors.

Again, the significance of weather and of biotic interaction has been brought to attention in connection with forestry problems and the attempt at reduction of the numbers of predatory animals, and the protection of certain species of game. Likewise the study of the effects of rodents on the beech seed crop in England in connection with dry years (952) under natural conditions. Korstion (493) emphasizes the effect of deer and other animals on the acorn crop.

2. Control of animals present

The fencing out (exclusion) of certain animals or fencing in (inclusion) has recently been a practice (885). Watt (952) uses an ingenious method of excluding some things and admitting others. McDougal (547) showed that the limits of certain cacti were determined by rodents by means of fencing. Pearson (662), Clements and the investigators at the Santa Rita Range Reserve have also fenced areas to exclude various wild animals as well as livestock.

A few investigators have introduced certain animals. McNab (unpublished) introduced earthworms into some soil and excluded them from other soil.

In the main these "experiments" should be compared with undisturbed areas wherever possible as a check upon abundance. Per-

manent quadrats (Clements (173–175), Cooper (209)) of large size and free from the experimental influence should be examined to check against general fluctuations in abundance, etc.

Wolcott (985) studied the amount of forage taken by insects in a pasture (deciduous forest area). To determine how much of the economic grasses and clovers the larger or more abundant phytophagous insects noted in the pasture were eating, Wolcott found it necessary to conduct feeding experiments. Expressing these data in terms of the weight of the insects themselves made possible direct comparisons with what the cows were getting from the pastures. Surprisingly enough, it was found that where few cows were in the pasture, the insects ate more of the grasses and clovers than the cows did. The cows obtained a larger share of the pasturage only when they kept the pasture so short that it afforded scanty protection for the crickets, grasshoppers, and leafhoppers, and was more attractive to the robins, who foraged there in greater numbers and further reduced the number of insects.

3. In water

In water biotic experiments have been more definite than on land. Numerous dams have been built, canals cut, etc., under conditions where an entirely new biota had to develop through the gradual processes of succession. We know of no case where any *thorough* study of this kind has been made. A little was done on the populating of the Kiel Canal (Bandt (112)). The municipal water-supply dam in the Sangamon River at Decatur, Illinois, was completed in 1921, and a large area of bottom land was inundated; by 1926 the original soil had been covered with river silt and the bottom appeared to be of the proper consistency to support many bottom forms. Yet only scattered chironomids were found. The bottom should have supported *Campeloma*, mussels, small snails, emphemerids, worms, and other aquatic insects. All were very local and all except the mussels were not common or not abundant. The mussels were restricted as to number of species. The shallower sandy bottom lacked snails such as *Pleurocera* and some small animals, though mussels were present. The characteristic aquatic vegetation was wanting. The vegetation and all the animals mentioned occur in some abundance in the river above the dam so that accessibility is an important feature of the case. Evidently succession is a slow process

even under the Decatur lake conditions. In these cases some practical significance is to be attached to the successional question, because the tendency is to plant fishes as soon as the water is impounded and before a plankton has had time to develop. The study of succession here would be of practical as well as scientific significance.

Wilson (980) studied bivalves on a wave-built terrace at the base of an eroded cliff and found that *Macoma nasuta* had moved seaward and *Mya arenaria* landward. This was indicated by the location of maximum abundance of old shells (from some year in which they were abundant) and living shells. This showed that these bivalves were influenced by depths. The terrace became flatter as the shore line moved landward. The *Mya* followed the shore line inward but the *Macoma* of necessity moved seaward to maintain themselves in the same depth of water because the terrace became wider and flatter due to erosion of the cliff and deposition below.

VII. BIOMETERS

Among primitive peoples and in the early periods of our civilization (pp. 4 and 14), plants and animals in their seasonal appearance, and abundance from season to season and from year to year, were the only indicators of the presence or approach of desired game and fish, of the time for seeding or prospect of abundance or failure of food for the coming season. Such primitive phenomenonology (phenology) like alchemy fell into disrepute and instruments were substituted. The imperfection of the results from these has led to a return to the use of organisms as indicators. The botanists who as a group were most severe in their condemnation of phenology have been recently most positive in their reacceptance of the underlying principle of organic indicators. Animals have long been used as indicators of conditions in water, especially as regards pollution. The writer has been especially impressed with the sharp distribution of animals in small streams when considered longitudinally and the hopelessness of measuring instrumentally the factors involved. The small streams tributary to Lake Michigan north of Chicago were studied repeatedly from 1906 to 1914, and a particular small stream near Muncie, Illinois, has been visited and the fauna studied once or twice a year, for twelve years. There have been surprising correlations between stream flow and general weather conditions and the animal communities present which would seem very difficult to correlate with instrumental readings had they been made.

Biometers are organisms which may be used as indicators of conditions or the suitability of a climate. McLean (564) grew certain plants for this purpose. In the old phenological work the blossoming of certain plants was found to be correlated with other phenomena.

Biometers are of two kinds, phytometers and zoömeters. Phytometers usually indicate conditions through variations in body size commonly referred to as yield. They also indicate by amount of seed production, seed germination, survival, number of individuals and adaptive response.

Zoömeters indicate through abundance or number of individuals. This constitutes their most important method of indicating. Survival, fecundity, size and rate of growth are important. Response affecting body form is less important in motile animals than in plants and sessile animals (see p. 71).

1. Phytometers

Clements and Goldsmith (179) have carried on phytometer studies over a six-year period. While the use of instruments in measuring the physical conditions of a habitat was regarded as essential by these investigators, it was obvious that there is no instrument which records the effect of the combined factors upon the plant. It is this lack which led to the use of plants themselves in an attempt to evaluate the various conditions under which they grew. A plant so used is called a phytometer. Phytometers are of various kinds according to use: (a) Group phytometers, such as quadrats; (b) Single phytometers, a single plant; (c) Natural phytometers, native plants are used; (d) Artificial phytometers, plants specially grown or transplanted; (e) Control phytometers, plants in containers; (f) Free phytometers, planted in the soil; (g) Climatic phytometers, placed in containers allowing the control of water and soil; (h) Edaphic phytometers, plants placed in different soils in the same local climate; (i) Long period phytometers; (j) Short period phytometers.

The responses of the plant which are measured are: (a) Transpiration (measured by water loss); (b) Photosynthesis; (c) Growth; (d) Adaptation (changes in form and structure). The plants most commonly used were: sunflower, pinto bean, Kherson oat, Marquis spring wheat, sweet clover, and wild raspberry.

Extensive studies were made of the Pikes Peak region from 1918

to 1923. (a) In this region, within a distance of seven miles, occur six climaxes. (b) Stations were established at a montane, a subalpine, and a plains area. (c) Results: (1) Transpiration was highest at the plains, lower at the montane, and lowest at the subalpine station. This factor did not vary consistently with any instrumental record. (2) The leaf area was usually greatest at the montane, and second at the plains station. (3) The water requirement generally decreases with increase in altitude. (4) The size of plants measured both by green and dry weights varies, the largest plants at times being produced at the montane and at other times at the plains station.

In 1923 the use of phytometers in the study of a single factor was attempted. The factor selected was light intensity. The stations were all within 100 yards of each other and at the same level. One station was in full sunshine, another in half-shade and the last in full shade. Sunflowers were used as phytometers. Studies were also made of slope exposure. Two stations were established on the opposite sides of Engelmann Canyon. The authors after six years' experience consider that the phytometer method is indispensable to all quantitative studies.

2. Zoömeters

The point of view in the cases in which zoömeters have been used is different from that in which phytometers are used. There is no consideration of communities.

The experience with sewage animals indicates that single organisms cannot generally be relied upon to indicate general conditions. Abundance of two or more associated species of a community may be considered of special significance. Jensen (438) and Blegvad (101) both found that all the species of the marine communities varied together (fig. 25).

The use of experimental methods such as transplantation, exclusion and inclusion, together with physiological experimentation, and contino
us observation of abundance will serve to establish certain organisms as indicators of value. Some insect pests may well serve as indicators of associated phenomena.

For example, abundance in the codling moth (Shelford (826)), is in part governed by fall rainfall and moderate winter temperature which leads to almost complete survival of hibernating larvae with dormancy overcome and the large surviving population in condition

to progress to pupation rapidly. The springs are moderately dry with more rain later in summer. Figure 62 shows the monthly rainfall and temperature for abundant and scarce years, with the actual range for three Illinois localities in 1926, a year in which they were unusually abundant. Isely and Ackerman (428) have suggested that temperature above 17°C. after sunset is favorable to egg-laying, but this idea had not been tested by comparison of abundant and non-abundant years.

VIII. CULTURAL ECOLOGY

Modern ecology, properly defined as the science of communities, must find community relations such as community structure, succession, annuation, etc. in the agricultural and other cultural conditions. Unless these are displayed there would be little justification for the use of the term. Natural history, physiology, etc., would be better terms. There is little justification for the term physical ecology; as presented it is usually merely physiology. There is evidence, however, that laws of succession, annuation and aspection can be worked out for soil and that the disturbance of waters by man's activity results in succession.

1. Ecology of agricultural lands

A personal communication from K. M. King indicates that there is a succession of soil animals in agricultural lands from the breaking of prairie to an old field, which will be of much significance economically. Morris (602) has shown that fertilizer added to soil increases the animal population.

Crop rotation to control insects is a practical recognition of succession. Sanderson (773) has said that this is one of the most important factors in insect control.

Forbes (308) has discussed the Indian corn plant and points out the heterogeneity of the insects associated with the plant under cultivation in Illinois, but does not take up the matter from a community standpoint. Teosinte or Mexican fodder grass from which it is supposed to have originated might help to illuminate the community relations of the plant and its pests. Knowledge of the origin of the plant under consideration is often helpful.

2. *Ecology of polluted and modified waters*

Richardson (733–735a) has shown a long series of retrogressive uccessions in the Illinois River because of pollution with Chicago ewage. The most important work on zoömeters or animal indiators has been on polluted waters. Here aquatic plants and aniials have long been used as indicators of pollution. Kolkwitz 489) and Richardson (735a) (see also 312, 972) used the following erms:

Kolkwitz	*Richardson*
1. Polysabrobic	1. Septic or saprobic
2. Mesosaprobic a	2. Pollutional
3. Mesosaprobic b	3. Sub-pollutional
4. Oligosaprobic	4. Clean water

Kolkwitz divides a stream starting from the source of pollution nto these four zones characterized by the various organisms as ndicators of the condition of the water. This use of zoömeters lepends upon a single species rather than a community of them. Richardson is convinced that such zones are recognized with diffiulty due to the overlapping of species. He shows this stringing ut and overlapping in the chironomid larvae and other forms as ne goes up or down the river.

IX. RESPONSES OF ANIMALS (194, 195, 583, 610)

The most often used response to yearly variations in weather is hat of the scales of fishes (fig. 30), shells of mollusca (fig. 31), and ike structures in other animals, which show bands corresponding to apid growth periods alternating with periods in which growth ceases. In such cases, the width of the rapid growth *ring* (fig. 30) varies with he length of the period and the favorability of the season, just as in he cross section of trees. As is the case with trees, interruption of growing conditions are likely to result in extra bands. In all cases the bands are usually annual, but secondary bands occur due to variations in conditions during the season. Creaser and others (193, 216, 356) summarize the literature and present results on American fresh-water fishes.

Murray and Hjort (610) called attention to the response of the skeletal parts and scales of fishes as indicators of age and growth.

Growth reflects temperature, length of season, quality and quantity of food, etc. They discuss the subject in the following terms:

> It has been discovered that in various boreal fishes the seasonal changes in their growth leave certain traces in all the osseous structures, such as vertebrae, gill-covers, otoliths, and scales, a difference being plainly seen between the parts formed during rapid growth (in summer), and the parts formed dur-

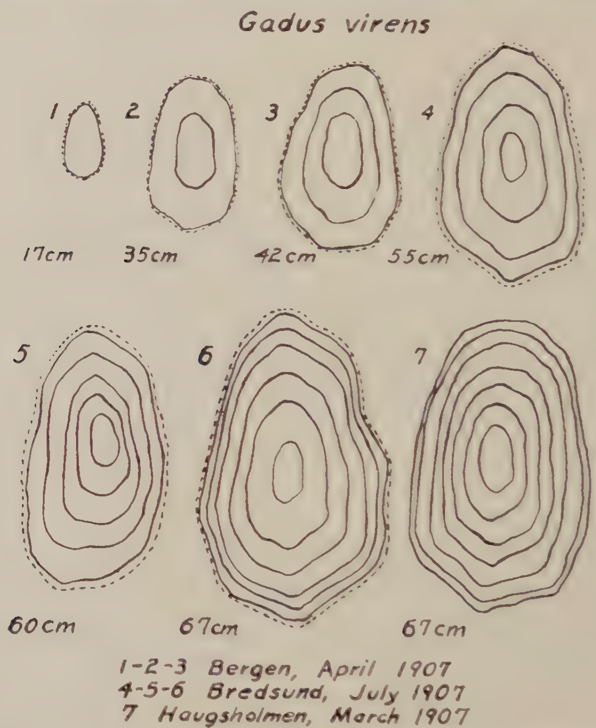


FIG. 30. Showing the growth rings of the scales of the saithe from Damas (after Murray and Hjort (610)).

> ing feeble growth (in winter). In this way visible rings or zones are formed in the structures mentioned, varying according to summer and winter, thus enabling us to count the number of winters and summers passed by the fish in question, and to ascertain its growth in various phases of life. This was first discovered by Hoffbauer in the scales of the carp (1899), and has also been observed to hold good in the case of the otoliths of the plaice (Reibisch), and of the scales of gadoids (Stuart Thomson), while Heincke and others have proved various bones to be good indicators of growth. A voluminous litera-

ture has accumulated as the result of these methods, which assumed greater importance when in 1904, upon the recommendation of Heincke, the international fishery investigators adopted them and applied them to many special and general problems. In recent years during the fishery investigations of several countries the growth and age of various commercial species have been subjected to analysis . . . . . By counting the winter-rings we can ascertain how many winters each fish has lived, and by examining a great number of individuals from a definite catch we may ascertain the number of individuals belonging to each annual class. . . . .

Some of the general results obtained by these investigations are of great interest; for instance, the growth of fishes has proved to be largely dependent on the temperature. Some chemical investigations corroborate this. . . . . The fat-contents of the sprat increase during summer, when there is a rise in temperature, while both decrease towards the end of the year; it follows from this that the growth of the fish must be influenced by the prevailing temperatures in different waters.

The investigations on the scales of fishes have now given us numerous facts confirming and elucidating this. Thus Damas says that the age of first maturity in the cod undoubtedly varies greatly according to local conditions. Generally the growth of cod-species may be said to decrease, and the age of first maturity to increase, the farther north we go. Thus on the Skagerrack coast a saithe may be 30 cm. long at the end of its first year, while a saithe of corresponding age in northern Norway is not, as a rule, more than 10 cm. in length. In northern waters, therefore, the winter-rings in the scales are much more marked than in more southern waters, for instance, in the North Sea. . .

While studying the growth of Gadidae, Damas conceived the idea that by examining the growth-history of single individuals, as depicted in their scales, one should be able to determine the localities, or at least the conditions, in which the individuals had grown up, in other words that this study should afford a key to the migrations of the fishes; thus he considers it probable that a certain saithe captured on the west coast of Norway may be recognized as having spent its infancy on the north coast of Norway. Similar ideas have been expressed by Lea after studying the scales of herring. He discovered that among the fat-herrings of northern Norway the ones born in 1904 could be seen to have had an exceedingly poor growth during their third year, the summer-belt in the scales being strikingly small in that year (see fig. 560). This peculiar feature was in that year limited to a certain part of the coast. The individuals thus "marked" were, however, in subsequent years when increasing in age found to have a much wider distribution, extending to the west coast of Norway and other localities. He considers this as significant of migration, and even attempts to calculate the percentage of the herrings taken on the west coast that had spent their infancy in northern Norway.

Shell-bearing mollusks show bands comparable to rapid and slow growth (fig. 31). The bands are commonly annual in this latitude.

Some ungulates, e.g., the bison and cattle, tend to show age by

rings on their horns. The number of prongs is considered an index of age in the deer, though *old* individuals are likely to have the prongs reduced again. In many mammals old and young individuals can be distinguished by the condition of the teeth, and in some cases by the number of teeth.

X. PHYSIOLOGICAL EXPERIMENTS IN NATURE

One of the most promising fields for experimentation lies in the modification of natural weather condition. (Clements and Goldsmith (179)). This, of course, is actually practical in the work on

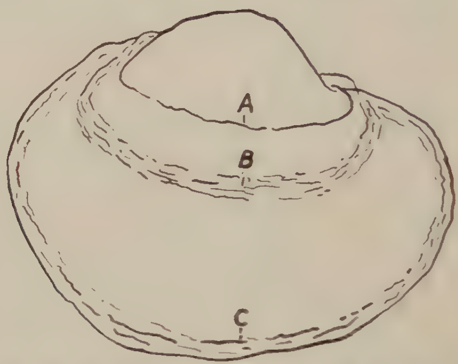


FIG. 31. A shell of the pocketbook, *Lampsilis ventricosa*, which was recovered after being measured and confined in a wire cage in the Mississippi River for two years, four and half months. The line *A*, an interruption ring, marks the size at the time of measuring. The lines *B* and *C* evidently correspond to the two periods of winter intervening. The inconspicuous sign of a winter interruption preceding the date of measurement does not appear in the drawing. Two-thirds natural size (after Lefevre and Curtis, Bull, U. S. B. F.).

insect pests, e.g., codling moth work where trees or other plants are screened in. The air circulation is impeded and the light reduced as shown by measurements with the Macbeth illuminometer. These enclosures are intended as controls relative to the condition in the open field. Caging of small animals for exclusion or inclusion is a serious problem which has not been solved; fine screen impedes air movement and reduces light. We know of no experiments where inclosure has been effected and at the same time these difficulties overcome. Many small animals, including many active insects, could be effectively retained by high fencing with screen which would reduce interference with light. Controls of this sort must be greatly improved and no doubt can be when attention is given to the subject.

1. *Experimentation without enclosures*

The following factors may be modified:

a. Light (a) may be reduced quantitatively and qualitatively by ion-selective and selective screening; (b) may be intensified by the ddition of artificial lights; (c) the day may be extended and cloudiess compensated for by artificial light.

b. Temperature may be increased by partially enclosing with glass r by other artificial means such as the discharge of warm air. Cold ir may also be discharged.

XI. LABORATORY EXPERIMENTS ON ANIMAL COMMUNITIES

A recent development in the study of populations inaugurated by 'earl (656) promises to afford much information on population laws n communities. Pearl grew Drosophila in pint bottles and found hat the population increased in the same manner as human populaion does. He then doubled the size of the bottles and found that he absolute size of the asymptotic population varies as the square f the volume of the universe in which it grows. He encountered nany difficulties in maintaining the food and all experiments eventully had to be abandoned because of these difficulties.

Recently Chapman (158) has taken up similar work on one of the our beetles. He cultivated the beetles in layers of flour 1 cm. deep, round especially fine and including all the wheat kernels. The opulation increased to a certain point and became stationary, when ach gram of flour contained the same definite number of beetles. 'he temperature, humidity and condition of the flour were mainained uniform. He thus established his formula $C = \frac{BP}{R}$. C s the population; R is the environmental resistance and BP potenial rate of the population increase.

The formula requires that the population finally become stationary. 'hapman (156, 158) has elaborated this field and cited Thompson 896–898), Muir (608), Woodruff (990), LeFroy (514).

The flour and dry grain feeding insects of which there are a dozen r more fairly common in the writer's latitude and an abundance of arer, more southerly, or occasional ones, afford interesting possiilities as to communities made up by bringing these species together.

After the initial laws of competition and population balance under different conditions of temperature and moisture, uniform and variable, have been established, they afford the possibility of introducing suitable predators and observing the results. There is a considerable number of species feeding upon various dry materials, including tobacco and wool (242, 410a, 731), that might be used in such work.

CHAPTER III

Behavior and Acclimation

I. INTRODUCTION

As has been indicated in the preceding chapter, observation of the behavior of biotic groups and of particular species is one of the methods necessarily followed. It affords promise on the biotic side, of giving results of the most far reaching character and importance. This field of endeavor can be greatly extended by the introduction of simple experimental methods to be employed in the field as supplementing the observations and affording a further evidence as to the factors involved in the action studied (141, 435, 436, 466, 469, 561, 717, 729, 730, 738, 959).

Behavior plays an important rôle in community and climatic relations, illustrated by reference to the migrations of birds, mammals, from north to south and from high to low altitude with the approach of winter. Cahn's theory involves hormones (141). There are also numerous migrations from vegetation to ground and from grassland to forest or shrubbery.

These behavior reactions, while they add to the difficulty of work with animals as compared with plants, bring about a condition wherein animals are a better index of conditions at any particular *time* than plants are.

Furthermore animals often maintain their positions in the environment by the constant play of behavior reactions. This applies especially to motile animals of seashore lines and rapid water, shifting sand and in the open waters of the sea and of lakes. Most motile animals stay in the same place so far as the general habitat[1] is concerned, but are active nevertheless. Some are actively destroying plants, leaves, stems, etc., some are burrowing into the ground and thus modifying conditions, and their activities are of much biotic importance. Some activities are supposed to be instinctive. Some are probably cultural, that is, taught to the young by the parents as is the case in birds and some mammals. The greater number are

[1] In ecology a habitat is an area and not a particular location.

more or less mechanical responses to physical and chemical conditions and their fluctuations or to the environment and community complex (808–812). Many of the instinctive and intelligent actions are ascertainable only by observation in nature and such observation is never to be neglected. Some animals are gregarious or have a tendency to aggregate in groups (17–20). The social and gregarious and probably traditional tendencies of animals have important effects upon biotic relations. This is well illustrated by the Kaibab deer which does not change its winter range to the available more favorable grounds even under the pressure of hunger and the efforts of the supervisors to move it.

Acclimation is also considered in this chapter because it commonly, though not necessarily, manifests itself in differences in behavior. Furthermore, the most accurate tests of acclimation involve laboratory study of reactions.

II. BEHAVIOR

A. Experimental field study

Experiments with noteworthy results have been performed by observers of animals in nature. These have consisted of simple changes in the surroundings, removal and replacement of landmarks, removal of the nest to another location, and damaging of the nest. Peckham (662a) found that digger wasps could not find their nests when the surrounding grass blades were removed. Herrick moved the nest of certain birds and observed the results (391). Such experiments should be performed as often as opportunity is afforded.

It is, however, possible to extend the field of outdoor behavior experimentation by the use of apparatus. Field, garden and enclosure experiments will undoubtedly come into far greater use in the immediate future than they have in the past. This will necessarily follow as fast as investigators come to realize the crudeness of the so-called critical laboratory experiments of the past and the inadequacy of the purely internal explanation of heredity, development and evolution.

It is possible and necessary to devise apparatus with which experiments can be done in nature to check and verify the inferences from the normal activity and the laboratory experiments. Reactions to natural physical and chemical forces serve to indicate the means by which animals maintain themselves in the biota, and indicate the

ysiological reason for the selection of place of abode. Such experi-
ents are further necessary in testing and verifying the efficiency of
uantitative methods.

The following methods have come within the experience of the
uthor (815) and proved important in the interpretation of biotic
lations (160). The possibility of extending and refining this type of
ork and methods is quite unlimited and awaits further applications
special problems for full development.

1. *Mechanical stimulation—shock and vibration* (57). Field experi-
entation ordinarily consists of careful observation of the normal
tivity of insects on plants for example, followed by a jarring of
plant on which some of the animals are found while another (the
ntrol) remains undisturbed. There are usually definite responses.
such a case, it shows the effect of the shock of a quantitative net
sed in sweeping, upon the movements of the animals. Their
action time may be estimated. Borrows (63), after noting the
fect on the response of a spider of the vibrating wing of a fly in
ntact with its web, applied experimental methods in further study
the response of spiders. He used tuning forks and an electric
brator.

2. *Reactions to soil and bottom material.* Animals which burrow
to or live upon soil or the bottom of bodies of water may be put
rough experimental tests with soil varied and surrounding air or
ater essentially unmodified. A suitable container for this purpose
nsists essentially of two pans soldered together as shown in figure 32,
other plan so as to give a ring-shaped space and no corners or
nter. These may be accompanied by a suitable control in the
me positions and with one kind of bottom or soil material while the
her has two or more.

This type of experiment may be varied to test reaction to soil and
ottom covering of débris vegetation, etc., often with very definite
sults. Field experiments may be performed with burrowing and
tten wood inhabiting animals, e.g., striking positive responses are
e rule with tiger beetle larvae when the abdomen is thrust into a
le in the soil, and with various insects living under bark when
milarly treated.

3. *Geotaxis.* Field observations of the orientation of animals
ch as the grasshopper, which usually orients with the head up, and
tydids, which usually orient with the head down, are profitable.

Aphids, many of which orient with the head down, may be inverted by bending the plant. In a half hour to an hour the position of a considerable number has usually been reversed. Some Chrysomelids always hang to leaves, etc., with their backs down. Usually consistent orientations or lack of the same may be noted and suitable modifications devised.

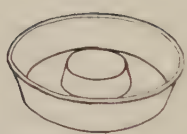


FIG. 32

FIG. 33

FIG. 32. Field rheotaxis pan with circular center for prevention of central eddy. Current is produced by the hand.

FIG. 33. *A* shows the ground plan of a field rheotaxis box. *B* shows an isometric drawing of a box.

4. Reactions to currents. (a) Anemotaxis. In the field, orientation of flies in the wind when it is not too strong can usually be noted. The rate of air movement may be measured with an anemometer, modified by a shield or accelerated by a fan.

(b) Rheotaxis (11, 57). (1) Field study with rheotaxis pans. Field study of rheotaxis for comparative purposes may be conducted

with the double pan (Figure 32) which consists of two pans, one 12 cm. and the other 30 cm. in diameter, soldered together. Similar animals with similar methods of locomotion such as swimming animals or creeping (11, 12) animals, may be used for field study as follows: Animals are collected from the rapids of a stream and from a near-by pond. A current may be made with the finger by passing it around the pan until a strong current is produced.

The following animals were secured from a brook: (1) Argia, brook damsel fly nymph, from under stones in rapids, (2) Hydropsyche, caddis worm from rapids, (3) May fly, from under stones in rapids.

The following animals were secured from a pond: (4) Haliplid beetle, (5) Corixids, (6) Small sunfish $\frac{3}{4}$-inch long.

The current was started with the finger, and when well underway, the hand removed and the order of orientation noted. At first the animals are swept around.

First reading: The animals oriented with heads toward the current in the following order: (1) Caddis fly larva, (2) Damsel fly nymph, (3) May fly, (4) Haliplid beetle, (5) Corixid, (6) Fish.

Second reading: The same, except the fish preceded the Corixid, 1, 2, 3, 4, 6, 5. (Numbers refer to list above.)

Third reading: Like second, except May fly last, 1, 2, 4, 5, 6, 3.

Fourth reading: Like second, 1, 2, 3, 4, 6, 5.

Fifth reading: Like second except Haliplid before damsel fly, 1, 4, 2, 3, 6, 5.

Thus on the whole the animals orient to the strength of current corresponding to that in which they live, with occasional irregularities.

(2) Field rheotaxis boxes (fig. 33). These are modeled after Allee's box. The large box is 63 cm. by 14 cm. by 14 cm. One-half of each end of the box is removed and replaced by screen. The end which is placed upstream is supplied with two semicircular partitions, the larger with a radius of 7 cm.; the smaller with a radius 1.25 cm. as shown in figure 33 *a* and *b*. These partitions are 5 cm. high and connected with two others which run to the end of the tank, 4 cm. apart. At the distance of 50 cm. from the semicircle the partitions bend to the corners of the box. Thus, with a screen to separate the long central part of the box from the end chambers, a box in which the animals may be confined and through which the water of the stream may flow, which is 4 by 50 cm. (which is the size of Allee's

current box), is provided. The partitions which make the sides of the central trough through which the water flows, make two side chambers, which, with the addition of screens, make chambers like the central trough, one of which may be filled with water and serve as control chamber.

This box is carried to a stream, and, after the investigator is familiar with the fauna and the habits of different species, the box is fixed in the stream, and the rate of flow through it is determined

TABLE 1

Showing the reactions of four species of stream animals to current in the field rheotaxis boxes when set in the rapids of the stream from which the animals were taken. The habitats of the animals are as follows: Hydropsyche, in rapids under and on stones; Corydalis, under stones in rapids; darters, among stones in rapids; minnows, in pools.

SPECIES	EXPERIMENT									CONTROL								
	Per cent resting on bottom	Per cent on upper screen	Per cent negative	Per cent indefinite	Per cent positive	Per cent on lower screen	Per cent of active indefinite	Per cent of active positive	Per cent of active negative	Per cent resting on bottom	Corresponding to per cent on upper screen	Corresponding to per cent negative	Corresponding to per cent indefinite	Corresponding to per cent positive	Corresponding to per cent on lower screen	Corresponding to per cent of active positive	Corresponding to per cent of active indefinite	Corresponding to per cent of active negative
10 Corydalis*......		4	0	0	22	74	0	100	0	0	27	10	0	11	52	47	0	53
10 Hydropsyche....		0	1	0	39	60	0	97	3	0	3	9	0	9	79	50	0	50
3 Etheostoma coerulum......	100	0	0	0	100	0	0	100	0	0	0	33	27	40	0	40	27	33
10 Notropis sp.....	0	0	0	0	100	0	0	100	0	0								

* Current 11 cm. per second.

by dropping in bits of paper or with a pitot tube (p. 432). Animals are placed in the experimental trough. The tendency to cling to the screen is noted, their speed of movement against the current, etc. The boxes are adjusted in the stream so as to give an amount of water and rate of flow suited to the animals at hand. The animals on the screen are not in a position to orient to the current and are usually clinging and inactive. Two (or one) categories are provided for the animals that are not reacting to the current, and three for the

nimals that are in the current: positive (+), indefinite (∞), and egative (−). The last three are for the animals that are active n the water or in the current on the bottom. (Table 1.)

Readings are taken at regular intervals of one second to three ninutes as a rule. The characteristics of the rapids community—namely, its strong tendency to cling to objects or rest on objects e.g., darters), and its very high percentage positive orientation in trong current—are demonstrated. A considerable amount of omparative work may be done. The animals of pools between apids in the stream such as fishes like Notropis and the darters may e compared. Both are strongly positive, but the darters rest on he bottom. With a strong current relative efficiency may be tested nd the darter found most effective.

The investigator may carry one of the long screen ended boxes used or keeping animals alive and another box which just goes inside of t but of nearly the same dimensions and with a glass bottom. If minnow is placed in the glass bottomed box with about 1 inch of vater and this is held securely in the hands and carefully moved rom left to right about 2 inches above a gravel covered shore. The ish turns about when the gravel appears to move from tail to head. There is some disturbance of the water however, but the experiment s highly suggestive of the sight orientation described by Lyon (544). A large screen-ended box is used to demonstrate the orientation f some of the larger fishes in the current.

5. Reactions to light. Field experiments.—The purpose of the xperiments performed differs materially from those of the investigators who would determine whether the animals react to irection or intensity, or who seek to determine the effect of light pon the organisms. In most of these experiments the purpose is to etermine the reactions of the animals to light, differing both in ntensity and direction and with the heat rays not screened out—in ther words, light as it affects animals in their natural environments.

Simple equipment consists in cake pans, 10 by 30 cm. at the bottom nd slightly larger at the top and 7 cm. deep painted with flat black aint, though much more elaborate and accurate apparatus may e designed (figs. 35–38). Tubes about 4.5 cm. in diameter (fig. 34), vith hemispherical ends and caps of the same shape slipping on so s to make the tube in place about 30 cm. long, are provided. These are painted flat black on one-third of the inside circumference,

which is placed downward in the experiments. Two pans, preferably two tubes and a thermometer are necessary. Covers for the pans are three in number; one is a simple tin box, deep enough to rest on the ground when over the pan (fig. 36); the other, a cover with an adjustable slit (fig. 37), and the third a holder (fig. 38) for a red, green and blue glass. The covers fit neatly one inside the other, the holder for glasses being smallest. The entire outfit may be packed inside the two covers, together with a thermometer, making a package of the size of the largest cover, which is conveniently carried in a book strap.

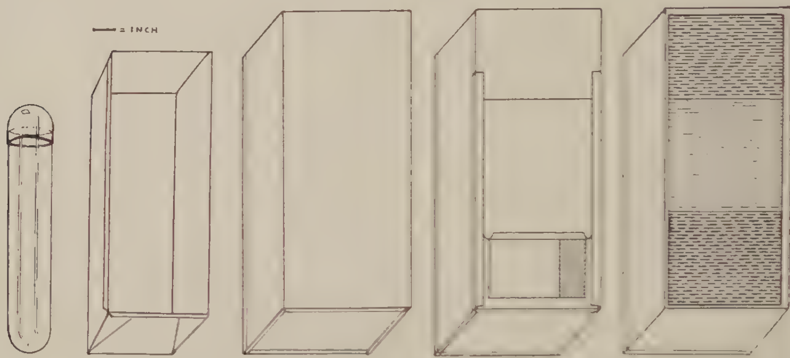


FIG. 34 FIG. 35 FIG. 36 FIG. 37 FIG. 38

FIG. 34. Field light tube with cap, for confining animals in light experiments.
FIG. 35. A cake pan.
FIG. 36. Cover without slit.
FIG. 37. Cover with slit for admitting light.
FIG. 38. Cover holder for the three colored glasses.

Experiments with light are conducted in a piece of primeval forest large enough to have a fauna characteristic of such woods. Here animals are observed and collected from the various levels or strata. In the experiments, usually for comparative results different animals are mixed together: some taken from under logs and bark and others from the herbaceous vegetation; another set, from the surface of the ground and from the shrubs or from the herbs and from the shrubs. A number of individuals of a particular species are usually brought together in one of the tubes by the experimenter, and then divided between two tubes, while a number of individuals from another stratum is prepared in the same way and mixed with these (or, if the angle of the sun is such that the two tubes can be exposed to the

ame light, they are both kept separated). A slit is opened in the litted cover so as to give an exposure of a part of the bottom of the

TABLE 2

'tudents' comparison of phototaxis of animals from different strata in beech woods. Experiments done in woods. L, light third; M, middle third; D, dark third. Figures, per cents of total individuals read. Five individuals, ten readings, every two minutes.

HABITAT	ANIMAL	L	M	D
. Under loose bark; subterranean stratum...	Centipeds	0	18	82
	Beetle larvae	4	0	96
. Ground stratum..........................	Frogs	16	52	32
. Herbs, field stratum (6 inches from ground)..	Spiders	42	13	45
. Shrub stratum (6 feet from ground).........	Leaf hoppers	70	30	0

TABLE 3

'omparison of phototaxis of animals of the same strata in woods and open roadside. L, light third; M, middle third; D, dark third. The figures are per cent of total individuals read. Five individuals, ten readings every two or five minutes.

HABITAT, STRATUM AND CONDITIONS	ANIMAL	PER CENT IN THIRDS		
		L	M	D
. Experiment in strong light (road):				
Ground; taken from woods........	Frog	10	36	54
Ground; taken from road..........	Grasshopper	70	12	18
a. Experiment in strong light (road):				
Herbs; from woods................	Flies	6	40	54
Herbs; from road..................	Treehoppers	50	25	25
b. Experiment in faint light (forest):				
Herbs; from woods................	Small leafhoppers	46	22	32
Herbs; from road..................	Large leafhoppers	28	34	28
a. Experiment in strong light (road):				
Shrubs; from woods...............	Mixed insects	54	18	28
Shrubs; from road.................	Mixed insects	78	2	20
b. Experiment in faint light:				
Shrubs; from woods...............	Mixed insects	49	16	35
Shrubs; from road.................	Mixed insects	58	42	0

ube to direct sunlight. The balance of the tube is divided into alves. The control is set up in the same way and completely

covered, except during readings. The control tubes are divided into three corresponding parts. The number of individuals in each part is recorded at definite intervals of one to five minutes and totaled at the end of the observation and reduced to per cent. (Table 2.)

On these excursions the investigator should carry a Wynne exposure meter in common use for photographic work or Macbeth illuminometer and compare the light intensity in the habitats of different animals in so far as is practicable.

A second type of study designed to show the differences in the physiological make-up of animals from different communities is shown in Table 3. Animals from the various levels of the forest are mixed with animals from the corresponding levels of the road and roadside. The species characteristic of the roadsides are commonly what is termed forest edge species.

A comparison of 1, 2a, and 3a, all performed in strong light, shows that the animals from the same strata in the roadside and forest differ strikingly in reactions. Grasshoppers from the road are positive and frogs from the woods are negative, etc. There is accordingly, a marked difference in the physiological character of the animals from the same level in different habitats. This equipment may be used, also, over warm and cold soil, for temperature experiments.

B. Laboratory study of behavior

For precision and analysis laboratory conditions are essential.

1. Gradients. The establishment of permanent repeatable gradients and other tests of behavior, e.g., for the purpose of determining whether or not changes in physiological states or the occurrence of acclimation have taken place, are essential.

(a) Current in water. This may be maintained and readily measured in the Allee straight current apparatus (fig. 39) Allee (11). Current gradients have not been developed but could easily be made by combining a series of supply tubes and straight current channels with metal partitions which are omitted at the point of study. Other apparatus for the study of reaction to current has been described by Lyon (544).

(b) Air movement, evaporation, humidity and temperature gradient. Figure 40 shows the apparatus used by Shelford (808), by Chenoweth (161), and by Hamilton (367) and others (385), to secure air flow gradients. The air enters through three slits and passes

across the cage and out through screens with a tight glass cover in place. The air movement may be regulated as rapid, medium and weak flows. A hood (fig. 41) is needed to cover the apparatus.

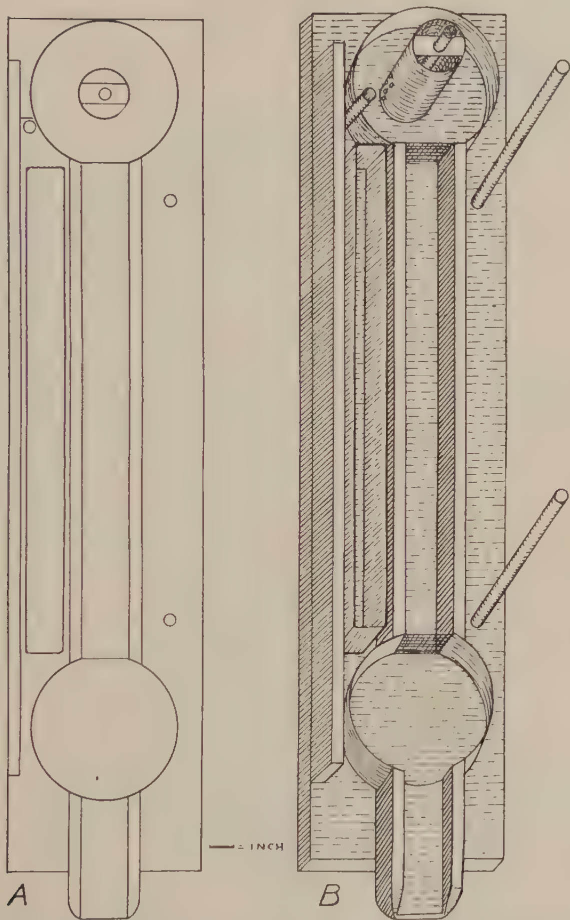


FIG. 39. Allee's straight current box. *A*, plan of box with control box cooling space along the side (815); *B*, an isometric drawing of the same. The posts are for supporting electric lights.

This same apparatus has been used successfully for air humidity experiments in which the air was treated in an apparatus similar to that shown in figure 43. Air temperature was used in the same device

in experiments on horned lizard by Weese. In this case cold water was run under the bottom of the cage to prevent reactions to bottom temperature.

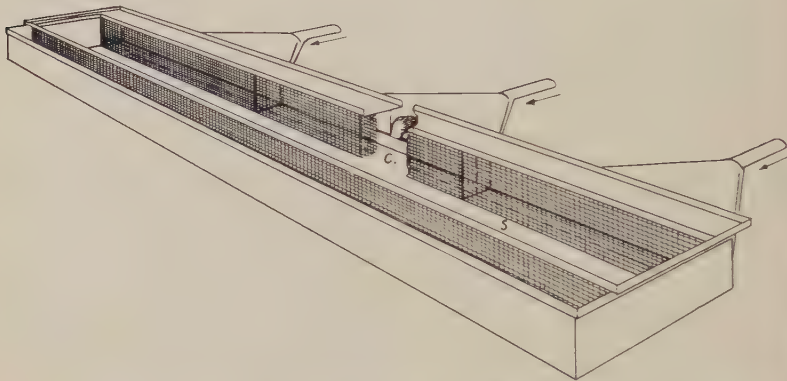


FIG. 40. Gradient cage with cover removed. S, space in which the animals are confined, C, cut to show diffusing screens and slit.

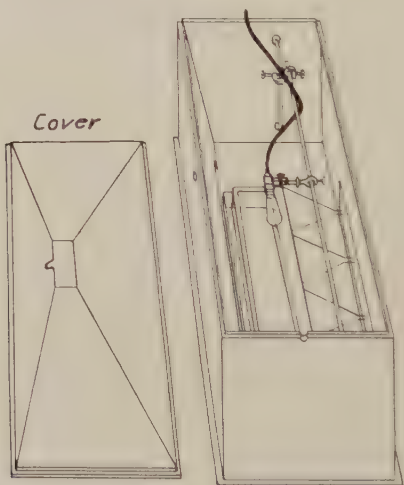


FIG. 41. Hood for excluding surrounding light from gradient cage

Johnson (452) devised a circular gradient (fig. 42) to eliminate the difficulties due to the contacts of the animals body with corners and ends. In this case two flows of medium air are used.

(c) Chemical gradients in water (828, 963, 837). Three chemical gradients in water were established in the manner shown in figure 44. Water of one kind ran in at one end and another kind at the other. Outflows being at the center, a gradient was established. Wells tested the gradients produced, by measuring the conductivity when a salt was being introduced at one end.

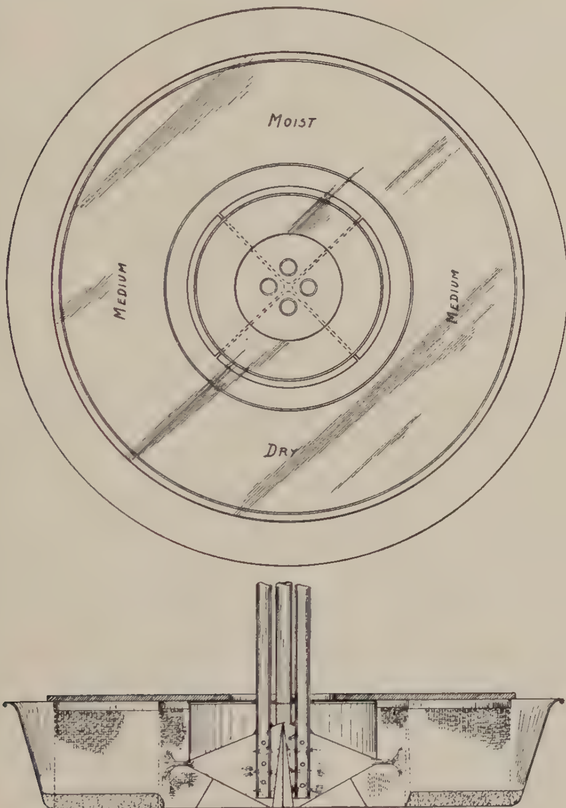


FIG. 42. Johnson's (452) circular air gradient cage without ends to confuse thigmotaxis and reaction to air conditions.

(d) Graphing of animal reaction (fig. 45). On a special ruling the distance between two lines is taken to represent the length of the gradient, a red line is the center, and blue lines divide the area into sixths. The use of a wide space is desirable with beginners, as

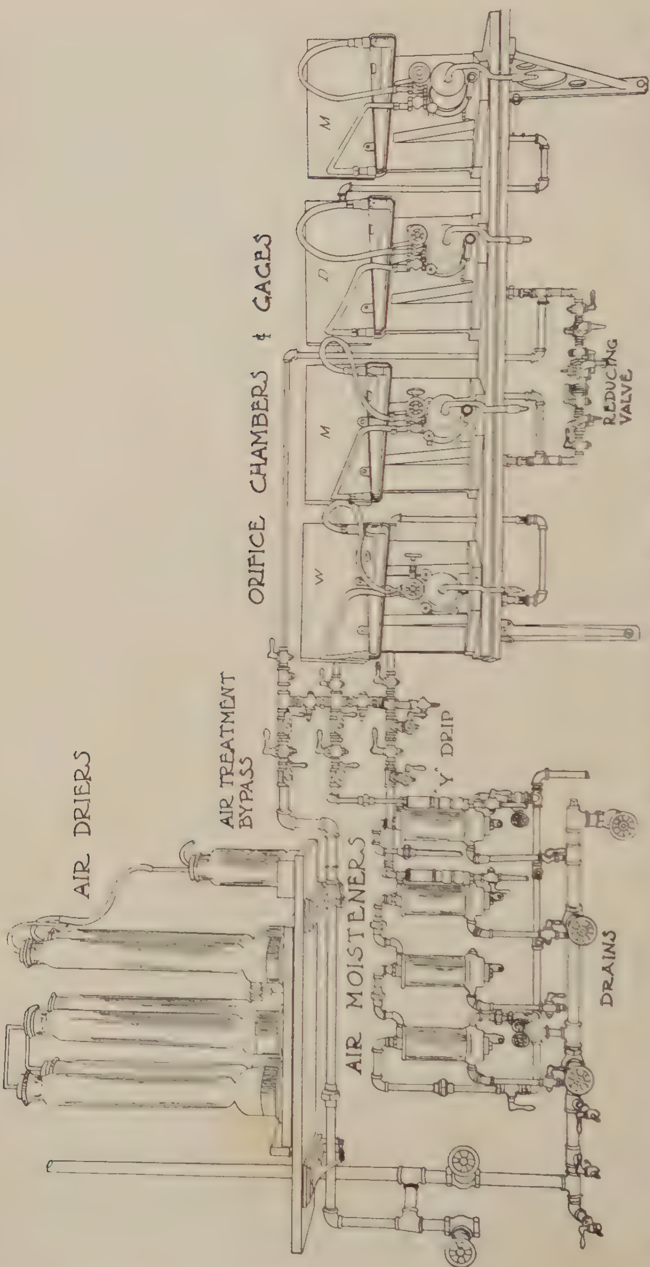


FIG. 43. Apparatus for controlling air conditions for short periods. The apparatus may be supplied with air dried by means of refrigeration or it may be dried with sulphuric acid in large chloride jars. Air is moistened by bubbling through water in air washers with bass wood strainers. The air enters the chamber through a center tube from the top and bubbles up inside a glass cylinder. The medium humid air is passed through one moistener and the moist air through three. The air is then passed through diaphragm chambers to measure rate of flow (see p. 241).

nuch more skill is required to graph accurately in a short space. The spaces between the horizontal lines on the special paper are ised to represent minutes. Figure 45 shows a typical graph. The

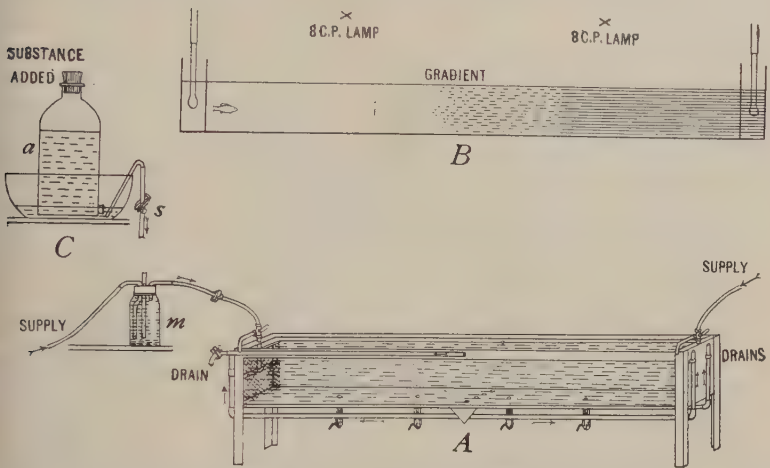


FIG. 44. Gradient tank (A). Longidutinal section of tank (B). A. The ;radient tank and apparatus for introducing substances into one end. The vater flows into the two ends of the tank from a common source. The flow is ıdjusted with a pinch cock on a rubber hose at the right-hand end, for ex-ımple, at 500 cc. per minute. This is done by turning the three-way valve o as to run the water outside of the tank through the small spout which ends ıt the water level just outside of the tank. The water can be caught here in a ;raduate for a definite length of time and the flow per minute determined. The low of water at the end into which the substance is added may be set at, say, 00 cc. per minute and then sufficient of the solution added to the bottle (m) rom the siphon above at the left (100 cc.) to make this 500 cc. also. The olution of a non-volatile substance is siphoned (see C) from a dish in which s a 12-liter aspirator bottle (a) with the upper opening tightly corked and the ower one open. When the water in the dish falls below the level of the lower pening a few bubbles of air slip in and the same amount of fluid flows out, thus naintaining a constant level in the dish as long as the supply in the aspirator ottle holds out. Volatile substances have usually been added directly from he lower opening of the aspirator bottle. In this case it is necessary to correct he flows occasionally The solution is run into a mixing bottle (m) which is onnected in the flow of pure water. B shows a longitudinal section of the ank when a substance is introduced at the right-hand end. The substance is hown by black markings. The central portion shows a gradient between ure water (white) and the introduced substance (black lines). The graphs re drawn on the basis of the position of the fish in this longitudinal section.

econd graph shows a sharp avoidance of neutral waters on the part f a herring. This gives a full detail of the movements of an animal or twenty minutes, of which the first fifteen are used here. The

readings for ten minutes are shown in table 4. The first method is obviously most nearly correct. These readings may be checked by placing a straight edge across the graph at appropriate time intervals and noting the position of the fish. Many cases show wider diver-

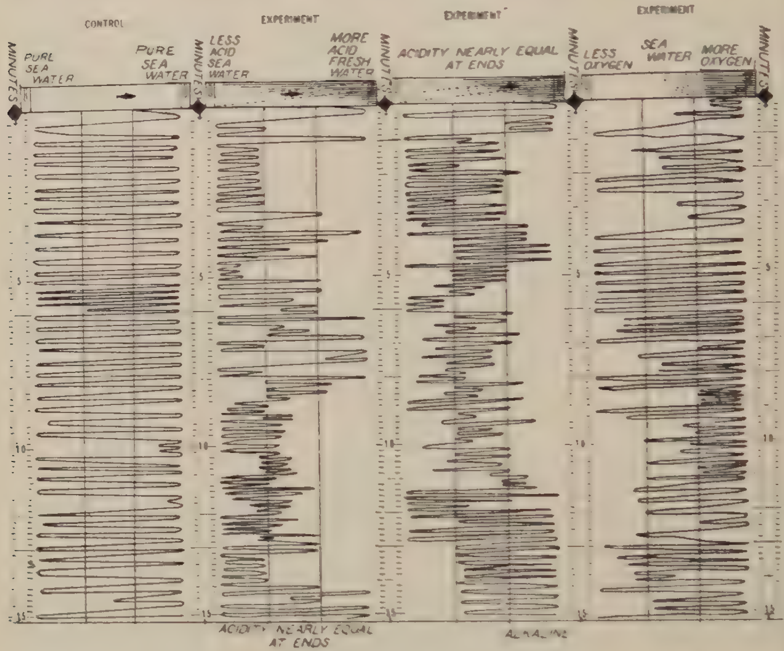


FIG. 45. Graph 1 shows the regular back-and-forth movement of a herring in pure water. Graphs 2 and 3 show the selection of a less acid water and the shifting of the position of the fish from the left to the right hand end as the acidity slowly changed. In this case the herring selected the alkaline fresh water, ignoring the salt which is important to marine animals. The fish was confined between inclined screens because of the difference in density of fresh and salt water. Graph 4 shows the selection of water with most oxygen by a herring. (From the Scientific Monthly.) Reactions to temperature are similar.

TABLE 4

Result of a ten-minute reading of graph 2

	PER CENT IN THIRDS		
Every half minute	60	25	15
Every minute	50	30	20
Every two minutes	20	60	20

ence with the different methods of reading, and serve to show the
eed of precision in taking down results.

Attention has been called (Shelford (810), Shelford and Allee (829),
helford (815)) to rapid modification of the behavior of these animals

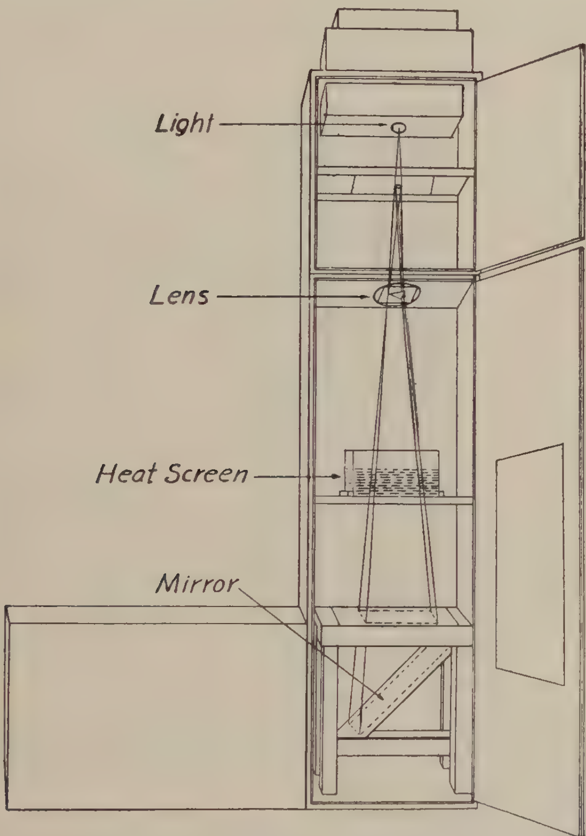


Fig. 46. Yerkes light grader (815) in vertical position. The light from a
trogen filled lamp is focused in one direction and not the other by a large
lindrical lens covered except for triangular opening. This gives an area of
tense light at one end grading to darkness at the other.

hich make good graphs. There is invasion of the generally avoided
nd but the distance traversed into this end becomes shorter with
ch repeated trial. This has been interpreted as rapid increase

in sensitivity. At the outset of this work with gradients too much dependence was placed on it for aquatic animals, as indicating where they would live or be found with reference to the stimulus in question. Acclimation appears to occur to a marked degree among aquatic animals, especially, and the method appears to be useful as one of the measures of acclimation rather than of habitat preference. It is not at all certain that the reactions of aquatic animals are a depend-

FIG. 47. Shows an oblique box partially combining a general direction with intensity; a graded beam of light passes through the glass sides. With this animals which are negative to direction will work their way into the dark, as well as those which are negative to intensity (815).

able indications of the habitat preference. Hall (364) found consistent reaction in young white fish correlated with the carbonate content of the water during the formation of the first blood cells.

(e) Light gradients. Yerkes light graders (fig. 46) as described by Mast (581) are provided in a dark room at the University of Illinois, but where dark rooms are not available, a dark box with a tower for the lamp has been used for some experiments. The most important modification of the Yerkes-Mast apparatus is the 45-

legree box (fig. 47) for holding animals. This was suggested in connection with experiments (809) in which it was found that, while ome stream animals react to direction of light and others to intenity, animals from the same community and stratum react in a similar nanner and all go into the dark, for example, when direction of ays guides them in same way as the decreasing intensity (fig. 47).

III. REGULATION

The terms regulation, acclimation, and acclimatization have been ised more or less interchangeably. In a general way, regulation akes place most quickly and acclimatization least quickly, though he processes may be one and the same or closely related. These processes of adjustment constitute an important phase of biological cience. The commonly recognized regulatory mechanisms are best understood and will be briefly outlined first.

1. Temperature regulation

a. Homoiothermal (warm-blooded) animals (59, 576). (a) Cold tmosphere or any condition which increases evaporation lowers body temperature. (b) Contraction of peripheral blood vessels concentrates the blood in the interior and keeps up the temperature of the vital organs. (c) Cold increases the metabolism and the production of heat counteracts its effects. (d) Warm atmosphere causes the expansion of peripheral vessels and the flow of blood to the xterior. (e) Warm atmosphere decreases metabolism and lowers he heat production. (f) Warm atmosphere causes the sweat glands o pour out water which evaporates, lowering the temperature in nimals with sweat glands. It causes panting as in dogs which gives evaporation from the mouth with the same effect. Buzzards nd domestic fowl hold out their wings in hot weather with a similar esult.

b. Poikilothermal (cold-blooded) animals (576). There is no rapidly operating regulatory mechanism. Changes in temperature cause changes in metabolism comparable to those in chemical reactions, hat is, usually roughly proportional to the temperature change. However, among the invertebrates, there are special cases of temperature regulation. The honey bee (597) affords an example. According to Wilson and Milum (978) bees begin formation of a cluster t about 18°C. which becomes fairly compact at 13°C. although

bees may be found singly at 10°C. The cluster contracts as the temperature of the outside of the cluster varies with the surroundings.

At or below 18°C. the bees are often unable to regulate the cluster temperature. According to Phillips and Demuth (674) when the temperature of a colony of undisturbed broodless bees is above 13.9°C. (57°F.) and below about 20.6°C. (69°F.) the bees are quiet and their temperature drifts with the outside temperature. At lower temperatures they form a compact cluster, and the temperature within it is raised by heat generated by the bees, partially by metabolic processes, but for the greater heat production required by very cold weather increased muscular activity takes place in the form of wing movement, shaking of body and rapid respiration. With rise of outside temperature, the temperature of the cluster drops to meet the outside temperature, with generation of heat reduced or even discontinued, unless it gets high enough to induce greater activity, as in flight. Chapman and France (159) and Armbruster (36) have stated other ideas.

Milum states further (personal communication) that the inverse relation of cluster temperatures to changes in the outside temperature does not always exist with outdoor wintered colonies with little or no protection when the outside temperature drops to points below 0°F. or is maintained for long periods at temperatures near 0°F. At such temperatures, the bees appear at times to be unable to raise or even maintain the cluster temperature, due to lack of stores within the cluster and their inability to break the cluster and move to a supply of honey, under which circumstances many poorly protected colonies eventually will perish if the low temperatures are long continued.

Milner and Demuth (597) found that, with bees in a respiration chamber, the expenditure of energy was reduced to a minimum by the maintenance of favorable temperatures and the avoidance of disturbing factors. The energy produced by the bees as measured by the carbon dioxide and water produced, and the oxygen consumed, is higher per unit of body weight than that of the average laborer.

2. Respiratory regulation

(a) Excess of oxygen is sometimes fatal but the excess must be great. As a rule and under environmental conditions, animals have a capacity for using only a certain amount, so that a small increase does not have any great effect.

(b) Deficiency of oxygen is usually compensated by an increased rate of respiratory movement. Some forms cease activity. Amoeba stops activity, which decreases respiratory demand.

(c) Respiratory regulation in taxonomic groups. In birds and mammals, lack of oxygen results in partial oxidation which produces a condition of acidity and increases respiratory movements. In the case of insects, Moore et al. (600, 601) noted that the heavy, practically non-volatile and non-toxic oils penetrated the tracheae and caused the death of the insects but that the tissues of such insects were not stained by *trypan blue* (which stains dead tissues but not living tissues) until ten, twenty, or more hours had elapsed. The insects were killed through mechanical action, by the stopping of the supply of oxygen.

Shafer (798) has shown that methylene blue or indigo carmine injected into the body of an insect, which is then placed in an atmosphere *free* from *oxygen*, is reduced to its leuco compound, so that the body of the insect becomes white or yellowish white. Upon being removed to the air, the stain is again oxidized, so that the body of the insect becomes blue. By this method Shafer showed that the insects whose tracheae had become filled with oil, either died from want of oxygen, or vapor of petroleum products prevented oxidation. These methods may prove useful in other ways.

(d) Fishes and probably other aquatic animals show changes in acidity and both respiratory center and direct gill regulation. Protoplasm is a marked reducing agent. Fishes and most invertebrates survive lack of oxygen best in the presence of substances like carbohydrates. In such cases the carbohydrates may use hydrogen from water and thus assist in releasing O_2. This capacity of the fish increases with the decrease of O_2. Carbon dioxide increases acidity, which increases the respiratory movements.

The use of the swim-bladder in regulation in some of the fishes is unique. Modern workers think a "gas gland" on the surface of the swim-bladder keeps the latter filled. Gas samples have been taken by hypodermic needle with special apparatus (366). Normal perch averaged 19.9 per cent oxygen and 0.63 per cent carbon dioxide. Carp had less oxygen and more carbon dioxide. In water of low oxygen content, percentage of oxygen decreased; but oxygen in the swim-bladder is not great enough to be an important source of supply to the fish. With increased pressure, the percentage of oxygen in

the swim-bladder is increased. With increased carbon dioxide in the surrounding water, the percentage of carbon dioxide in the swim-bladder increased. The volume of the fish is also increased. This change brings the fish to the surface, where the proportion of carbon dioxide is less. When gas samples are taken from the swim-bladder at intervals, the percentage of oxygen increases in bass and perch; in carp the change is only slight, perhaps because carp has an open duct from the swim-bladder (366). In bass, the oxygen tension in the swim-bladder is greater than in the blood; hence, there must be active secretion, not merely diffusion of gases. Under increased pressure, the hydrogen ion concentration ("acidity") of the gas gland is increased. This results in more complete oxygen dissociation of blood in the capillaries of the gland, thus making "secretion" possible. The vagus nerve, also, has been shown to exercise control over gas secretion in the swim-bladder. Some investigators have shown that the lungs of man secrete oxygen under high-altitude conditions.

3. Neutrality regulation (386, 387)

Neutrality regulation is brought about by the capacity of bicarbonates and acid phosphates (buffers) to neutralize the strong acids with a small change in free hydrogen ions. In regulation more rapid respiration removes the CO_2 almost at once, and supplies more oxygen which facilitates oxidation of heavy acids. The amount of buffer may be increased, which usually requires time. Powers and Shipe (698, see also 444) found, however, that in certain fishes this time was much less than that required in vertebrates where more alkali is probably retained by the kidney (386, 976). Among fishes there are various suggestions of acclimation as indicated by the fishes found by Jewell and associates in very acid water and the occurrence of ordinary fishes in alkaline lakes. It is true, however, that fishes are differently affected by the different acids causing the difference in pH. As shown by Stickney (864) aquatic insects may not be affected by acid and alkali.

4. Enzyme and anti-body regulation (935)[2]

(a) Dog fed on starch produces digestive juices rich in starch-digesting enzymes.

[2] For further discussion see Chapter VI, pages 164-168, esp. 166.

(b) Change to meat diet and the character of the enzymes changes roportionally.

(c) Anti-bodies usually occur in animals and the amount is merely icreased by the toxins. They may be developed by feeding animals vith specific poisons. Feeding animals with bacterial toxins produces ntitoxins but is much less effective than injection.

5. Permeability and osmotic pressure regulation

In living frog skin the direction of easiest transfer of fluid subtances is from without inward. The rapidity of intake depends upon he vitality of the frog. It also depends upon the character of the ubstance; stimulants increase the intake; depressing agents decrease t or may cause a reversal. In dead skin, the transfer was most apid in the opposite direction (722).

a. Land animals. Excretory organs are permeable to salts such as NaCl, when present in excess, and the excess is quickly reduced. Even a dose of salts makes one thirsty because of the withdrawal of vater into the alimentary canal. Thirst is primarily due to increased smotic pressure, and is a means of water content and osmotic oressure regulation. Aquatic animals, e.g., fishes, excrete salt as do and animals.

Changes in permeability may serve to regulate osmotic pressure. Osterhout has found that alkalies (OH-ions) increase permeability. Acids first cause a rapid decrease in permeability followed by a rapid ncrease. Mixtures neutralize ("antagonize") each other. Thus acids added to isotonic solutions cause muscles to take up water, orobably due to the increased permeability causing salts to diffuse in. Salts diffuse through protoplasm less rapidly, thus KCl inhibits heart action. The velocity of inhibition is directly proportional o the concentration of salt. (See pp. 436–443.)

6. Water regulation (287)

Rowntree (750) has discussed the water balance in the higher mammals but largely from a medical standpoint. Thirst is important in supplying water and the kidneys in removing it. Birds kept without water lose weight, but the less essential parts lose water most rapidly.

Bodine (107) found that grasshoppers reduce their water content

to 65 per cent under cold weather conditions. Meal worms fed on bran, dried at 105°C. and kept in air without moisture maintained weight with only slight losses. Some died and at once dried up, losing weight rapidly (Berger (77)). Important studies of water relations have recently been made by Robinson (742).

7. Freezing point regulation (654)

Payne studied freezing points of Synchroidae, Pyrochroidae, Elateridae and various Cerambycidae, collected throughout the year. Oak borers were used for freezing point determinations on account of their natural exposure to low temperatures. The freezing point of the oak borer group lowers in winter and rises in the spring to very near that of water by mid summer.

Hardening, or cold resistance, occurs periodically with the seasons out-of-doors, but can be induced or broken up under experimental conditions by exposures to certain temperatures or moistures.

IV. ACCLIMATION

a. Temperature. Dallinger (235) produced acclimation of protozoa to 70°C. by raising the temperature gradually through a period of several years. Vernon (926–928) states that effects of heat are not accounted for by the amount of water in the tissues, but in the ovum of Strongylocentrotus the death temperature increases with the increase in the percentage of water. According to Loeb and Wasteneys (534) resistance to temperature varies quite directly with the concentration of the salts of sodium, potassium and calcium in sea water. The effect is not due to osmosis but to some unknown action of the salts present.

An intermittent exposure to a high temperature is just as effective an immunizing factor as a prolonged exposure. Fish subjected to high temperatures are immunized to still higher temperatures. They usually retained this immunity after being replaced in temperature low for a time (377). Mayer (589) found that death by heating was not due to lack of oxygen, but probably to the accumulation of the acid (H_2CO_3) in the tissues.

Davenport and Castle (237) produced acclimation of tadpoles to a temperature of 43°C. by exposure to 24.5° for four weeks. The theory is that acclimation is due to decreased water content of tissues.

Behre (71) shows that acclimation takes place in Planaria, in

experiments using the susceptibility to KCN, the colorimetric and biometer, determination of carbon dioxide, and head regeneration methods, all of which show the same general results.

Physiologically young animals show a higher susceptibility to the change in conditions and are also able to become more rapidly and completely acclimated to changes which are not too extreme. This is demonstrable throughout the animal kingdom (241).

Jacobs (430) has studied acclimation to temperature. He used three methods of attaining a given high temperature, viz.:

(1) Sudden exposure.

(2) Gradual change of temperature at a uniform rate (best method).

(3) Gradual change at a constantly decreasing rate.

Jacobs also devised methods of calculating death points. If the calculated death point coincides with the actual death point then no acclimatization has taken place. If the actual death point is higher than that calculated then acclimation has taken place.

The temperature coefficient of the species being studied is Q_1.

$$Q_1 = \frac{L_o}{L_{o+1}} = \frac{\text{Length of life at a temperature of } (n) \text{ degrees}}{\text{Length of life at } (n) \text{ degrees} + 1.}$$

In Starfish larvae eighteen to forty-eight hours old, Q_1 is 2. In *Paramoecium caudatum,* Q_1 varies more but equals approximately 3.

An example, using starfish larvae, may be described as follows: Q_1 determined as above, is 2.06. In experiments at 34° the fatal exposure is 420 seconds which makes the injury in unit time (one minute):

$$\frac{60}{420} \text{ or } 0.14$$

To find injury in unit time at 37°:

$$p = 37° - 34° = 3°$$

$$I_p = .14 \times (2.06)^3 = 1.2 = \text{injury in unit time at } 37°\text{C.}$$

When the above relations are known together with the time to death at a number of selected temperatures it is possible to calculate the point at which the death theoretically occurs when the temperature is raised at a uniform rate, also the degree of injury at a given temperature. The constants Q_1 and I_0 are essential. The degree

of injury which is inflicted by an exposure of any length short of the death point may also be calculated.

In the latter case, the amount of injury is represented graphically by the area under the curve $y = aQ_1^x$ (Fig. 48) in which "a" is a constant equal to the amount of injury, I_0, inflicted in unit time at a temperature selected for comparison, Q_1 is used as a constant, and "x" is an exponent governing the curve. From the figure it can be seen that the area of each individual rectangle is equal to its altitude

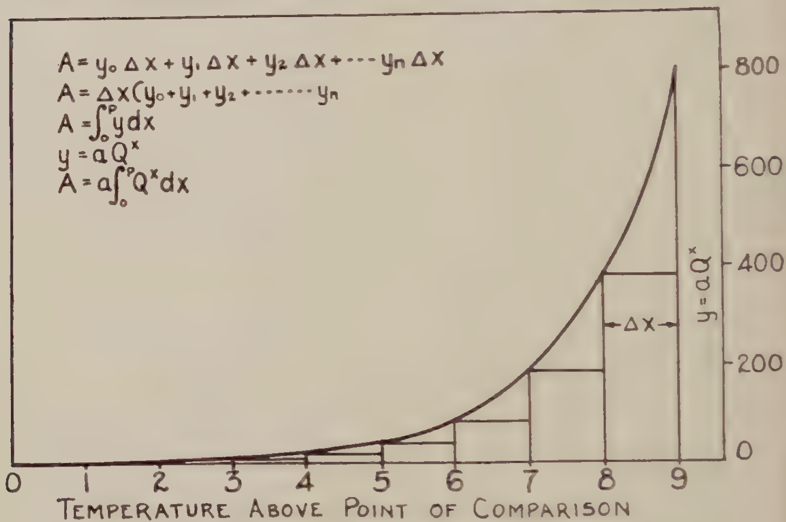


FIG. 48. Jacobs' injury curve (430). The Q of the figure is Q_1.

times ΔX, its width. If ΔX is chosen small enough and the rectangles are added together the total area will be approximated. Algebraically:

$$A = y_0\,\Delta x + y_1\,\Delta x + y_2\,\Delta x + \text{- - -}\ yn\,\Delta x$$
$$= \Delta x\,(y_0 + y_1 + y_2 + \text{- - - -}\ yn)$$

If ΔX is allowed to become so small as to approach zero, the true area under the curve will be obtained. Let us note Jacobs' procedure:

This may be expressed mathematically

$$A = \Sigma\, ydx$$

here Σ means "summation of"

$$A = \int y dx$$

r

$$\frac{L}{\Delta x \rightarrow O}$$

ut $y = a\, Q_1^x$ so $A = a \int Q_1^x\, dx$

If the curve is drawn between the limits $x = -b$ (room temperature) and $= p$ (the highest temperature attained), b and p, of course, being measured rom the temperature selected as the point of comparison, the integral becomes lefinite, or

$$A = I = a \int_{-b}^{p} Q_1^x\, dx = a\left(\frac{Q_1^p}{\log_e Q_1} - \frac{Q_1^{-b}}{\log_e Q_1}\right)$$

Since b (the number of degrees the room temperature lies below the tempera-ure chosen for comparison) is relatively large, the second half of the expres-ion within the parentheses becomes negligibly small and may be disregarded. This is equivalent to calculating the injury that would be inflicted in a rise rom an infinitely low temperature instead of from room temperature, but this mounts to practically the same thing, since even considerably above room emperature the injury inflicted in any ordinary time has ceased to be appre-iable.

If instead of raising the temperature at the rate of 1° per minute as implied n the calculation just given, the rate had been slower, say 1° in t minutes, the ight-hand side of the equation would have to be multiplied by t. The general expression therefore for the area, A, which represents the total injury, I, nflicted up to the temperature p° when the rate of rise is one degree in t min-utes becomes (when a is replaced by its equivalent I_0):

$$I = t\, I_0 \cdot \frac{Q_1^p}{\log_e Q_1}$$

In the case of starfish larvae where Q_1 is equal to approximately 2.0 and $\log_e Q_1$ therefore to approximately 0.7 we have finally:

$$I = t\, I_0 \cdot \frac{2^p}{0.7}$$

In case it is desired to know how high the temperature would have to be raised to inflict just fatal injury, it is only necessary to substitute for I the numerical value 1.0 and solve the equation for p. In such cases (taking $\log_{10} 2 = 0.3$).

$$p = \frac{\log_{10}\left(\dfrac{0.7}{t\, I_0}\right)}{0.3}$$

The results of applying this method to a gradual and regular rate of temperature increase in the case of starfish larvae are shown in table 5. In the first column is given the rate at which the temperature was raised, in the second the observed death point, and in the third the point at which death ought theoretically to have occurred (i.e., the point at which the area enclosed by the curve becomes unity) when the value of the constant, Q_1, was taken as equal to 2 (this value holding approximately for all of the starfish larvae studied). The value of I_0, which varies somewhat for different lots of larvae according to age, etc., was determined especially for the animals used in these experiments, and was found to be 0.05 at the temperature (33°C.) chosen for comparison.

Starfish larvae showed no acclimation. Paramoecium showed a great amount of acclimation. The "surplus resistance" gained by

TABLE 5

Temperatures at which death of starfish larvae occurred after varying rates of temperature increase from a starting point of approximately 20°C.

RATE OF TEMPERATURE INCREASE IN DEGREES PER MINUTE	OBSERVED DEATH TEMPERATURE	THEORETICAL DEATH TEMPERATURE CALCULATED FROM $Q_1 = 2.0$	THEORETICAL DEATH TEMPERATURE CALCULATED FROM $Q_1 = 2.2$
1°C. in 1.8 minutes	About one-third dead at 36.0°	36.0°	35.8°
1°C. in 4 minutes	35.0°	34.8°	34.8°
1°C. in 5 minutes	34.5°	34.5°	34.5°
1°C. in 8 minutes	All living at 33.5°, all dead at 34.0°	33.8°	33.9°

the starfish during the rise in temperature was practically zero; that of the Paramoecium was as high as 43. In other words the Paramoecium withstood 44 times the theoretical fatal injury.

While there is no doubt that mammals acclimate to temperature to some degree, little is known as to what is involved.

b. Changes in O_2 and CO_2 pressure. Low atmospheric pressures are met with on mountains, high plateaus, and balloon or aeroplane ascents. Mountain sickness effects are due mainly to the diminished O_2 pressure and consequent insufficient O_2 pressure in the blood and resulting disturbance. The volume of air breathed is increased, due simply to the stimulus of anoxemia. Acclimation to high altitudes consists in an increase in number of red corpuscles per unit volume. The average percentage of hemoglobin varies inversely with the barometric pressure. Oxygen secretion is developed in

he same manner as with the exercise of all other physiological unctions (362).

V. ACCLIMATIZATION

This term is commonly applied where several generations are iecessary to bring about the changes. On the whole it is an uncerain subject. It may not happen except through the selection of variations accidentally suited to the conditions. Various breeds of attle and sheep are best suited to certain regions. In some cases is in sheep, the conditions are like those in the place of origin of the breed, but in cattle physiological relations to climate as indicated by the distribution of breeds and by milk products production have been brought about largely through qualities correlated with other haracters selected in developing the breeds (Davidson (239)). Thus he Herefords were developed in the drier parts of England, but the adaptation to arid America on the part of this breed appears to be correlated with a genetic constitution adapting them to *scant pastures and severe conditions.* The Aberdeen Angus were developed in a still less rainy climate, at least so far as certain months are concerned, but were coddled and fed and are not suited to arid areas.

a. Methods of ascertaining the occurrence and degrees of acclimation. Three principal classes of test of regulation, acclimation and acclimatization can be recognized.

(1) The survival test consists in a comparison of the survival of animals kept under unusual conditions, with those not so treated. The test should usually be run in the adverse conditions.

(2) The success test may be defined as a test of anything which makes for the success of the species as an expanding population or as viewed from the standpoint of its culture by man. This includes survival and fecundity in the environment being tested, both in general and in adverse years and seasons.

In animals under culture, the rapidity of growth of young, the production of suitable flesh, wool, hair, milk products, afford the criteria. Facts ascertained by the methods used by Johnson (448) and by Davidson (239) should be fully checked experimentally both in so far as possible in the laboratory, and also by carefully planned transplantation experiments.

(3) Behavior selection tests involve the comparison of animals which have been subjected to adverse or unusual conditions in per-

manent measured gradients of environmental factors. While the experimental conditions should be so measured as to make the experiments distinctly repeatable, the *mixing of marked acclimated and unacclimated* animals in the same gradient gives a special check of unusual value especially if it follows similar uniform treatment in conditions as nearly optimum as possible for both. Some special cases were taken up in connection with the discussion of behavior. As many as are practicable of these tests should be applied in all cases. Chemical tests such as the use of susceptibility to poison may also be of value at times.

CHAPTER IV

Food and Food Effects

I. INTRODUCTION

The importance of food as a determining factor in the success of organisms has become increasingly apparent as knowledge has advanced in recent years. We now know that food may vary significantly in quality in hitherto wholly unexpected ways. It is evident that food effects require special experimental attention. While not directly a part of climatology, the supply of food for animals under observation must be considered for two reasons, namely: (a) the quality and quantity of food may be greatly affected by weather conditions, and (b) food effects must be eliminated from the effects of physical conditions in experiments. Furthermore, the food of animals is subject to many variations. For example, the fruit flies (Drosophila) and domestic cattle have been shown to be able to utilize flesh instead of plant food. As a general principle, animals eat more or less selectively from that which is available in the place in which they are living. It is very important that a study of the food habits of animals under experimentation be made with a view to determining the following things:

(1) The normal food of the species under consideration and the feasibility of introducing such food into the experimental conditions.

(2) The elementary food substances needed—such as salts, nitrogen, vitamines, or dissolved and particulate matter in water and organic matter in soil.

(3) The important necessary small organisms such as fungi, bacteria, etc., and plankton organisms in water.

(4) The effect of the experimental conditions on the food itself, especially when produced where the animals are kept, or grown in unusual conditions. (Treated in Chapter V.)

(5) The effect of quantity of food, especially where rates of growth are involved.

(6) The effect of the experimental conditions on the rate of food consumption.

When all these things have received adequate attention, it will still be necessary or advisable frequently to run checks in which normal out-of-door conditions remain unvaried and the usual food is contrasted with that necessarily used in the experimental conditions. To date, far too few animals have been reared in captivity, but material progress has been made on a few organisms, notably rats (632–633), mice, fruit flies, termites, protozoa, domestic animals,

TABLE 6

Showing the effect of the quantity of food (number of tadpoles) on the rate of development of the larvae of Dytiscus marginalis L. (from Blunck (102))

INSTAR	TEMPERATURE	NUMBER OF TADPOLES PER DAY, LENGTH 16 MM. FOR INSTARS 1 AND 2, AND 20 TO 25 MM. FOR INSTAR 3	LENGTH OF INSTAR
	°C.		days
1	18	4–7	6
	18	2–3	7–8
	18	1	9–10
2	19	6–7	5–6
	19	5	7
	19	3–4	7–8
	19	2	14
3	17–18	20–30	14
	17–18	12–14	21–28
	17–18	10	28–35
	17–18	6–7	35
	17–18	4–5	42
	17–18	2	49
	17–18	1	56

and fishes. Experiences with these afford suggestions as to food essentials and their variation.

II. QUANTITY OF FOOD AND MAINTENANCE (37, 102, 632)

Quantity of food influences rate of development and size. Periods of starvation have been studied in some animals and found to have important effects. The ability to withstand such conditions and to start growing after a period of standstill (maintenance) is quite remarkable. A food threshold, or maintenance ration, is that food

ntake at which a normally growing animal retains a constant aver-
ge weight.

1. *Regular restricted rations during development*

a. Rate of development. Although there has been little quantita-
ive work done on lower animals, it is well known that quantity of
ood affects rate of development. Blunck (102) did a series of ex-

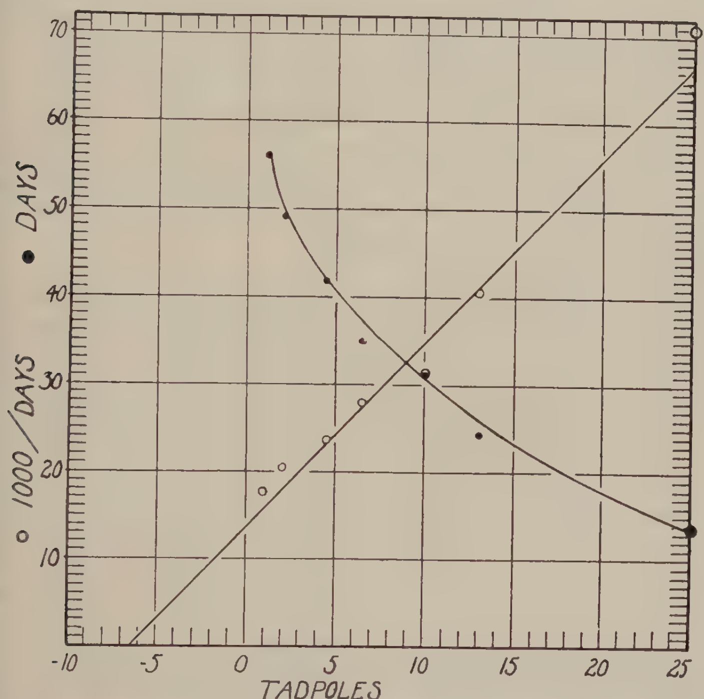


FIG. 49. Time (length of larval stages) and reciprocals of time plotted
ainst number of tadpoles eaten by Dytiscus larvae. Data from experiments
rate of development of Dytiscus marginalis by Blunck (102).

riments on the rate of development of *Dytiscus marginalis* when
d a varying number of tadpoles. Table 6 shows the results for
ree instars. If the reciprocal of the time is plotted against the
mber of tadpoles, a curve is produced which indicates that the
ects are not comparable to temperature (fig. 49). The points do
t fall in a straight line, and there is no suggestion of what the
aintenance ration may be.

Northrup (626) has shown that the length of the larval period of the fruit fly varies with the amount of yeast, showing that the retardation may be due to shortage of specific food substance while the general quantity apparently remains the same.

b. Maintenance in insects. These experiments, as well as those on starvation by Wodsedalek (982), indicate that larvae may be "maintained" for some time, at least, without growth or loss of weight. Little has been done on other land arthropods and lower animals but it is evident that there is a food threshold or maintenance quantity for growth whether the maintenance can be continued for any considerable period or not.

c. Maintenance in birds and mammals. Osborne and Mendel (632) working on white rats (257), concluded that "food may be either qualitatively or quantitatively deficient and cause standstill in the development of mammals." They show (p. 101) the following methods of producing standstill:

> (1) By under-feeding with rations of suitable qualitative make-up; (2) by the use of diets containing an adequate protein but with inorganic salt supplied in the form of a mixture of pure chemicals together with sucrose and starch as the carbohydrate component; (3) by restricting the protein content of the dietary below the minimum required for growth; (4) by furnishing, as the exclusive source of nitrogenous intake, proteins which lack some amino-acid group indispensable to growth. The protein lacking was probably one of the vitamins. The animals were maintained at practically the same weight and they retained their power to grow long past the age at which growth normally ceases (335 days) and for periods equal to half the normal life of the species, which is 1000 days.

2. *Starvation, especially during development*

Because food failures or loss of appetite not infrequently occur in experiments, it is important to know the effects of intermittent feeding and periods of starvation.

a. Insects. Silkworms, after fourth molt, were fed for different numbers of days and the effects tabulated by Kellogg and Bell (468), who summarized their results as follows:

> From these results it may be said that silkworms may be cut off from a food supply nearly seven days before the normal limit of their feeding time and yet complete their development (spin, pupate, and emerge as imagoes). These seven days represent a little more than half of the last intermoulting actively feeding period, or about one-ninth of the whole larval (feeding) life. The

eprivation of food for from one to four days seems neither to hasten the etamorphosis nor to modify it appreciably, nor to result in the production of moth of lessened size or lessened fertility. The larvae deprived of food not ore than four days before normal close of feeding time do not immediately in and pupate, but wait restlessly for the normal time of pupation (approxiately twelve days after the fourth moulting), and then normally spin and ıpate. If deprived of food for more than four days and less than seven, the rvae shorten their last intermoulting stage to about seven days, forming, owever, a normal cocoon and transforming into a normal moth. If the larvae e deprived of food eight days or more before their normal spinning-up time, ey invariably die without forming a cocoon, and in only one case was pupaon accomplished. A beginning at spinning is made by larvae fed more than vo days after the fourth moulting, but no spinning at all is done by larvae eprived of food from the day of fourth moulting or from the first or second ıy thereafter.

Non-feeding stages, no doubt, should be mentioned in connection ith starvation. Loss of weight during non-feeding stages of insect e is the rule. Kellogg and Bell (468) report that there is a slight ıt steady loss of weight from day to day through the entire pupal eriod, the total loss for the silkworm pupa amounting to about 14 er cent and that for the pupae of the tent caterpillar (*Clisiocampa* .), checkered-spot butterfly (*Melitaea* sp.), and mourning-cloak ıtterfly (*Euvanessa antiopa*) ranging as high as 35 per cent and en 65 per cent.

In grasshoppers, Bodine (107, 108) found that losses in body weight ıring starvation are marked, and that they increase progressively, starvation proceeds, up to a maximum for the species. Starvaon in the grasshopper results in a rapid loss in water content, which s a decidedly quick and fatal effect. Respiratory rates for insects e considerably higher than those for other animals. The rate of O_2 output differs for different species and is correlated with their odes of life. Increased temperatures cause increased respiratory tes up to 38°C. The value of Q_{10} varies, being highest (1.5) at ° to 25° and lowest (1.1) at 0° to 10°. The actual amount of CO_2 ven off by an animal decreases during successive periods of starvaon. Males show the higher output of CO_2. Feeding starved imals increases the CO_2 output. The data presented seem to incate that insect physiology has many points in common with that mammals.

Wodsedalek (982) made starvation experiments on the larvae of e dermestid museum pest, *Trogederma tarsale*. A number of speci-

mens varying in size from newly-hatched to practically full-grown larvae were placed in individual vials for the purpose of ascertaining the period of time that they could live without food, with results as shown in table 7.

The specimens were subjected to disturbance due to transportation from one laboratory to another, which undoubtedly increased the metabolism, as was evidenced by "the moulting of practically every individual toward the end of the trip or within a few days after it, and by the decided decrease in the dimensions of the larvae immediately following such a moult."

One of the most interesting phases of these experiments was the gradual decrease in size of the individual specimens. Many of the

TABLE 7

SPECIMENS	LIVED WITHOUT FOOD
Newly hatched without ever having eaten at all	4 months
One-quarter grown	14 months
One-half grown	3 years
Three-quarters grown	4 years
Full grown:	
Mostly	Over 4 years
Several	$4\frac{1}{2}$ years
Last	5 years, 1 month, 29 days, or 1884 days

largest larvae, which were about 8 mm. in length, dwindled down to practically the hatching length before dying. "Some of the largest larvae have been reduced to about 1/600 of their maximum larval mass."

Another phenomenon, even more interesting, is the fact that when the starved specimens almost reach the smallest size possible and are then given plenty of food, they again begin increasing in size. At the time of writing, a number of half-grown and larger larvae were undergoing the fourth and third "childhood" after repetition of feasting and fasting four and three times respectively. They reached the minimum and maximum sizes possible.

The above facts are introduced, in part, to show that cessation from feeding may influence the rate of development, the length of instars, etc. It is possible that such cessation may take place under

'avorable, but necessary, experimental conditions or when food is 'avorable. This is a possible source of error and should be guarded iinst.

Che amount of food eaten under different temperature conditions ows the same general laws as the rate of development described in ail in Chapter VII. A series of preliminary experiments on lepi-oterous larvae made in our laboratory further emphasized the ieral correspondence between rate of development and activity. thaway's recent work on fish study shows similar results (376).

. *Birds, mammals and fishes.* Osborne and Mendel (633), work- on white rats, showed that the impulse or capacity to grow can retained by young rats far beyond the age at which growth or-arily ceases. This capacity has a bearing on the effect of starva-1 for moderately long periods. Greene (347) has shown that the stored in the muscles of salmon is reabsorbed during the fast of gration.

III. QUALITY OF FOOD

1. Elementary food substances

Che green plants are able to build up all their complicated proteins, ;ars, and fats from nitrates, phosphates, and sulphates, on the hand, and from CO_2 on the other hand. Those microörganisms ich can not form sugar or starch from CO_2 are able to form all their teins from an ammonium salt or a single amino-acid. This onishing synthetic power is in sharp contrast to the behavior of mmals, which can not grow unless provided with one or more teins (Osborn and Mendel, (632)).

Rogers (743) has recently summarized the work on food and calls ention to the fact that Peters (668) has shown that *Colpodium* live in a sterile medium with inorganic salts and very minute ntities of histidine, arginine, leucine, and ammonium lactate:

'arious modifications of the culture fluid were made. The experiments 1 to indicate that, when the single amino-acids, histidine, arginine, leu-, are supplied, there is a much more rapid growth than when tryptophane ven; also that galactose and fructose, but not maltose, can be substituted glucose, in the medium. As would be expected, no growth will take place he absence of phosphate. Ammonium glycerophosphate (Kahlbaum) was id to serve as a complete source of nitrogen, carbon, and phosphate. nonium glycerate plus ammonium phosphate will serve in the same way.

Nitrogen, therefore, need not be supplied in a form more elaborate than ammonia.

Cleveland (181–183) has shown that cellulose (as well as wood) is a sufficient diet for termites and hence little or no nitrogen is required. These termites, however, can not live if their intestinal protozoan fauna is removed (182).

Loeb (529) conducted experiments to determine the simplest constituents required for growth and completion of the life-cycle in an insect. Fruit fly larvae were reared in the following solution:

Grape sugar	0.5 gram
Cane sugar	0.5 gram
Ammonium tartrate	0.1 gram
Citric acid	0.05 gram
K_2HPO_4	0.005 gram
$MgSO_4$	0.005 gram
H_2O	3.000 cc.

The experiments show that without any NaCl or $CaCl_2$ other than that which may appear as impurities in the chemicals used, five and probably indefinite generations of flies can be raised. The only salts added were K_2HPO_4 and $MgSO_4$. Numerous control experiments made in glass vessels showed that without either the addition of K or PO_4 no larvae can be raised. It was not certain whether Mg and SO_4 are as indispensable as K and PO_4, since in K_2HPO_4 alone a fly occasionally developed. It is certain, however, that the addition of $MgSO_4$ greatly increased the number of flies raised. As far as the evidence from these experiments goes, it can be said that muscular activity is possible either without any Na or Ca, or with only such traces as appear in the form of impurities in the chemically pure substances. K as well as PO_4, and also SO_4, and Mg, must be added to the culture medium in appreciable quantity. The fruit fly is independent of the existence of the green plants.

Loeb (529) states that the work of Winogradski and of Godlewski indicated that the nitrite and nitrate bacteria are capable of forming carbohydrates from CO_2 (or possibly other carbon compounds in the air) independently of light, and lead him to assume that the same may be true for certain other microörganisms.

To further test the possibility of flies living without microörganisms, sterile flies were transferred by Loeb and Northrup (531) to the following media: filter paper, cane sugar, $MgSO_4$, $KHSO_4$, NaCl,

$CaCl_2$, and nitrogenous compounds. The last class included each of the following: casein, edestin, egg albumen, milk, and mixture of leucine, alanine, glycine, asparagine, tryosine, tryptophane, and histidine. The results were the same in all cases. Some larvae reached full size, but did not metamorphose. Sterile banana was used, and the larvae grew slowly; few pupated; adults were about one-quarter normal size, and very little pigmented. No second generation could be raised. The addition of butter, nucleic acid, thymus or thyroid extract to the synthetic media was without effect. These experiments show that the fruit fly, when freed from micro-organisms, can not be raised successfully on sterilized banana or on a mixture of pure protein sugars, salts, and fat. Yeast was the only substance adequate as food for the larvae. Yeast, therefore, must contain some substance required for their growth.

This substance must be rather resistant to heat, since yeast heated for one hour at 120°C. is an excellent culture medium. It can not be salts or cane or grape sugar, since non-sterile flies grow normally on Pasteur media, as shown by Loeb. It has been shown by several authors that the fruit fly, freed from microörganisms and raised under aseptic conditions, grows more normally when yeast is present. Northrup (626) found that the number of flies which are able to develop on a definite quantity of yeast may be increased by the addition of banana, casein, or sugar to yeast. These latter substances, therefore, can serve as food for the larvae when supplemented with yeast. The rate of growth of the larvae is equally, or slightly more, rapid on mixtures of banana and yeast containing more than 33 per cent yeast than it is on yeast alone. In mixtures containing less than this amount of yeast, growth becomes slower as the amount of yeast is decreased, and finally, when the proportion of yeast is very small, becomes abnormal. Yeast, therefore, contains a sufficient excess of the necessary substances to render available as food approximately twice its weight of banana. What these substances are, is not yet known.

Northrup further showed that kidney, liver, and pancreas from the dog, liver from the mouse, and the bodies of the flies themselves are an adequate source of food for the larvae. Sterilized spleen, heart muscle, blood, adrenal, and thyroid from the dog are not an adequate food for the larvae. Muscle, testis, and tumor from the mouse are also inadequate. Sterilized thymus from the dog, rabbit, or calf

allow a few imagoes to develop, but growth is slow and the flies are abnormally small. No effect on the rate of growth can be noted when tethelin is added to the food.

The source of nitrogenous compounds required for growth and for completion of the life cycle in Drosophila is significant. Filter paper, although it contained only 0.02 gram of nitrogen, or 1/2000 to 1/1500 part of the total nitrogenous content of culture medium, seemed to have some influence. When glass beads were substituted for filter paper, "the yield of larvae was very much smaller than with

TABLE 8

Showing the length of larval life of the silk moth (Bombyx mori) in nature; from Bachmetjew (50, p. 699)

FOOD PLANTS	OBSERVER	LENGTH OF LARVAL STAGES
		days
Cultivated mulberry	In general	29–33
Cudraenia triloba	Sasaki	29–33
Broussonetia Kaempferi (paper mulberry)	Iwanow	40
Morus sorten	Iwanow	28
Lettuce	Kellog and Bell	90
Scorzonera hispanica	Schelkow	33–51
Scorzonera hispanica	Iwanow	39
Scorzonera hispanica	Tichomirowa	27
Scorzonera hispanica, first year	Hartz	54–62
Scorzonera hispanica, second year	Hartz	44–54
Scorzonera hispanica, third year	Hartz	42–56
Scorzonera hispanica, fourth year	Hartz	38–64

filter paper," although the larvae ate little if any of the filter paper.

From a quantitative viewpoint, vitamins are of much importance. Sherman (835) and Rogers (743) have summarized this field.

2. Variations in the quality of food plants

Quality of plant food has been studied chiefly in connection with food plants. Some phytophaga voluntarily feed upon several plants or may be forced to eat various plants, with resulting differences in size, color, fertility, or general success. Food plants have been analyzed only roughly as a rule. Most of these analyses have to do with the silk moth, brown tail moth, and other species of note-

orthy economic importance. Much of this literature, while generlly suggestive, lacks sharp correlation between the condition of the isects and the analyses and indicates inadequate control of other onditions. Grevillius (355) gives analyses of the various food plants f the brown tail moth. Bachmetjew (50) presents tables showing ariations in nitrogen, water, and ash of mulberry leaves grown in

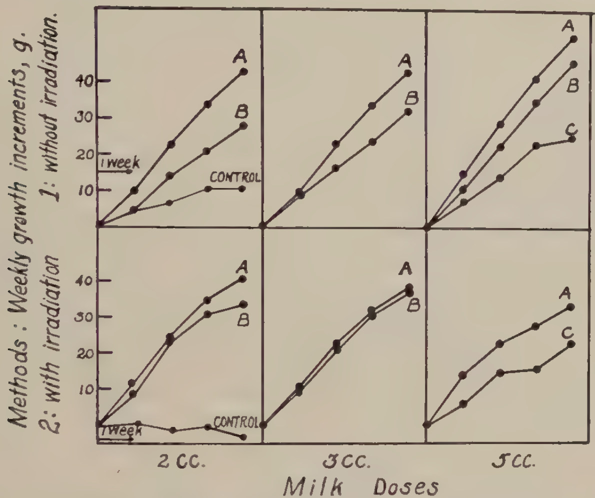


FIG. 50. The growth promoting value of milk. *A*, milk from a pasture fed ow; *B*, green food in dark stall; *C*, winter food in dark. Doses varying from to 5 cc as indicated. The curves represent the average degree of restoration growth (measured in grams of increase in body-weight per week) in young ts during the period in which milk doses were given.

In method *1* the milk doses were given after body-weight had become ationary on diet F, deprived of fat-soluble vitamins; the growth observed due to the joint effect of vitamins A and D contained in the milk.

In method *2* the milk doses were given when body-weight had become ationary on diet F, vitamin D being supplied by irradiation: the growth oserved is a measure of vitamin A only. (From data by Chick and Roscoe 62, diet F, p. 633).)

idely different localities (p. 707) and in leaves at different seasons nd from trees on different soils (p. 708); also detailed analyses of a umber of plants which may be eaten by the silk moth larva. Characteristics of first leaves of plants differ with varieties; first leaves winter rye, approximate dry weight in sugar is 40 per cent and of oring rye 33 per cent (Walster (939)).

Table 45 on page 371 shows the correlation between rainfall and

length of time the codling moth larvae spend in the apple. In picked apples, the time is reduced to 86 per cent of the average for apples on the tree; and the greater the rainfall, the longer the time in the apple. This is probably due to difference in the quality of the food. Further effects may be found cited under food and feeding of various animal groups (p. 118). The quality of light and duration of exposure have important effects upon the qualities of food plants.

3. *Variations in the quality of animal food*

The effects of conditions on some kinds of animal food are well shown by studies on milk by Luce (536, 537, 538), and by Chick and Roscoe (162)). The amount of vitamin A in cows' milk is largely controlled by the amount of green food. This was tested by the growth produced in young rats (see fig. 50). The amount of anti-rachitic vitamin (D) was found by Chick and Roscoe to be largely influenced by the insolation of the cow. Accordingly, milk does not constitute a uniform food, and the result on the rate of growth and on the condition of the mice was striking. Whether the flesh of animals varies in a similar fashion is another question (754, 755).

IV. FOOD OF AQUATIC ORGANISMS

1. *Dissolved and suspended organic matter*

Pütter (708) claimed that an animal absorbs organic matter from solution. Moore and others (599) repeated his work and disagreed with him in the matter of absorption of food. They found that sea-water did not contain dissolved and suspended matter in excess of 1 to 2 mgm. per liter. Their conclusions are summarized as follows: In these experiments the authors went a long way toward proving (1) that it is not necessary for marine animals to use the dissolved organic matter of the sea water, (2) that this factor is almost negligible, and (3) that the organisms actually increase rather than decrease the amount of organic matter in solution in the water in which they are kept.

The subject, however, has been investigated recently for fresh water and the question re-opened by Birge and Juday (91, 234). They summarized their findings and those of Frankland and Armstrong in the following terms:

A very large series of determinations of the amount of organic carbon and iitrogen in fresh water is to be found in the sixth report of the English comnission on pollution of rivers, presented to Parliament in 1874 (House of Commons Documents, 1874, vol. 33). This report contains many hundreds of leterminations of organic carbon and nitrogen from potable waters, made by Frankland and Armstrong. Twenty-three lake waters were examined, chiefly rom soft-water lakes. The mean amount of organic carbon found in these vaters is 2.30 mgm. per liter; the organic nitrogen is 0.314 mgm. per liter; he nitrogen-carbon ratio is N:C::1:7.2. If the organic matter is computed n the same basis as in the present paper, the result is nitrogenous, 1.96 mgm. er liter; non-nitrogenous, 2.80 mgm. per liter; total organic matter, 4.76 mgm. er liter.

The water of Lake Mendota contains in its plankton an average of about .140 mgm. per liter of nitrogen and about 0.990 mgm. of organic carbon. The residues from large samples of evaporated water, from which the plankton as been extracted, yield an average of about 0.393 mgm. per liter of organic itrogen and about 5.80 mgm. of organic carbon. The nitrogen and carbon rom the residues are called "dissolved."

The residues from the water of Lake Mendota yield ether extract to an verage amount of more than 0.5 mgm. per liter of water (0.564 mgm.). Green ake and Lake Geneva yield comparable, though smaller, quantities.

Part of the organic matter in the residues is, no doubt, particulate, but most f it seems to be dissolved. The quantitative relation of these two classes eeds further investigation.

The crude protein of the residues may be computed from the nitrogen (factor .25), and the organic carbon may be distributed to proteins (assigning them 3 per cent C) and to non-nitrogenous matter (computed as 45 per cent C); if he ether extract has been determined, the non-nitrogenous matter may be ivided into fats (75 per cent C) and carbohydrates (45 per cent C). The verage difference between these two methods of computation is about 3 per ent of the total organic matter.

On the first basis of computation, the water of Lake Mendota contains an verage of nearly 14 mgm. per liter of organic matter, of which about oneenth is in the plankton. On the second basis, and employing for the plankton he larger average results of the plankton report, the total is nearly 15 mgm. er liter of water of which less than 2 mgm. are in the plankton.

The average nitrogen-carbon ratio in the plankton is about 1 to 6; in the issolved matter it is about 1 to 14 or 15. In both cases the figures are subject o much variation.

The average dissolved protein is from three to six times as great as that of he plankton; the dissolved non-nitrogenous material is about 10 times as reat.

Studies of residues from twelve other lakes and two rivers show conditions ssentially similar to those of Mendota, both in regard to plankton and disolved organic matter.

The question of the fundamental food supply of the lake must be reexamined n view of the presence of these relatively large amounts of dissolved organic atter.

Experiments along this line have not given definite conclusions as yet. The processes are involved, and the methods (chemical) are regarded as open to some questions. However, the experiments throw doubt upon the policy of filtering much of the organic food supply out of water, as is the common practice in recirculating water systems.

a. Particulate matter. This has been held to be of great importance in the nourishment of the oyster, sponges, mussels, etc., (Johnstone (454)). The work of Blegvad (99) on the Danish marine bottom animal communities is, however, of special interest, because the animal communities worked over have been described from a modern ecological viewpoint, and because the food relations have been considered from an ecological viewpoint; furthermore, the methods used to make the determinations involved no station building, but the use of a boat. Blegvad summarizes his results in the following terms:

> In looking through the Danish animal communities one by one, as described by Dr. Petersen (669), it will be seen that practically all the characteristic animals, i.e., the most common and most evenly distributed forms are pure detritus eaters. This is, for instance, the case with all the bivalves, the extraordinarily numerous Spatangidae, many worms, crustaceans (e.g., *Haploops tubicola*) and gastropods such as *Aporrhais* and *Turritella*. Next in order of frequency come the herbivorous detritus eaters, among which the small gastropods of the plant region are especially important. The animals mentioned may be called producers in contra-distinction to the remainder, the consumers, and we find that the proportion between producers and consumers in all the Danish animal communities invariably shows a distinct superiority of the former. There is nothing surprising in the discovery that the purely carnivorous animals are relatively least common in the Danish communities, since they are forced to live by preying on other animals. Among the producers there are some forms which when fully grown are rarely, if ever, eaten by other animals, viz., the large detritus-eating Spatangidae: *Brissopsis*, *Echinocardium* and *Spatangus*. In addition, a number of large bivalves: *Cyprina islandica*, *Modiola modiolus*, *Pecten* and *Mya* sp., *Mytilus*, *Cardium*, and oysters, besides gastropods such as *Turritella*, *Aporrhais*, and large *Littorina littorea*, crustaceans such as lobsters and *Balani*, worms as *Arenicola marina* (in the shallowest water), and, finally, Anthozoa such as *Alcyonium digitatum*, *Pennatula phosphorea* and *Virgularia mirabilis*.
>
> The main result of the present investigations may be briefly summed up as follows: Detritus forms the principal food of nearly all the invertebrate animals of the sea bottom, next in order of importance being plant food from fresh benthos plants. The value of the live phytoplankton in this connection is absolutely minimal, amounting in any case to nothing more than an indirect significance through the medium of the plankton copepods.

2. Food of plankton animals

a. Fresh water.[1] According to Naumann (612), plankton crustacea re divisible into (a) forms which obtain their food by filtering the rater, and (b) forms which are predaceous and capture their food.)nly species of the genera *Leptodora, Polyphemus,* and *Bythotrephes* apture their food.

(a) Cladocera. The great majority of the cladocerans filter their ood from the water as they swim about. The filter functions in an mpartial manner. Even the particles of inorganic debris are filtered ut, going directly to the alimentary canal without sorting. Cladoera evidently do not have a sense of taste, as shown by the impartial nanner of taking the inorganic debris into the alimentary canal. In his manner the smallest algae are obtained, only the very small agellates about the size of bacteria escaping. Floating detritus, omposed of particles from shore, bottom, and plankton forms, is a ood material for cladocerans. The different species were studied in mall chambers observed with the microscope. Waters containing rdinary pond debris, carmine, india ink, various algae, and fine umus were used. With a carmine suspension, *Daphnia, Cerioaphnia* and *Bosmina* completely filled their intestine in a short ime. *Polyphemus,* which catches its food, when treated in the same ray for a much longer period of time, did not show any carmine in he alimentary canal. *Daphnia,* when placed in a culture of fine uspended humus, generally soon filled the intestine and, in ordinary rater to all appearances free of debris, soon had the intestine partially lled.

To test the rate of filling in relation to the size of the debris, *Bosnina* was treated to the following substances and the time for filling he intestine noted.

	minutes
Small algae	15
Terra silicea	60
Bacteria	240

Daphnia passed algae through the intestine in about fifteen mintes, apparently not digesting or assimilating any of them. Birge nd Juday (91) use this as one point in favor of the theory of utiliation of the dissolved protein, etc., of the water.

[1] Prepared with the assistance of Samuel Eddy.

(b) Copepods. The following analyses of intestinal contents of copepods were made under natural conditions, by Naumann:

Cyclops. A yellow mass—pieces of Entomostraca and jaws of Conochilus.
Diaptomus. A yellow finely-grained mass, with some algae.
Heterocope. A fine yellow mass, with a single alga.
Nauplii. A very fine yellow mass, with a single alga.

When the same species were placed in a carmine-india ink suspension, *Diaptomus* and *Nauplii* seemed to be the only ones consuming the ink.

Cyclops. Very slight trace of carmine-india ink in intestine.
Diaptomus. Full of carmine-india ink in intestine.
Heterocope. Very little carmine-india ink in the intestine.
Nauplii. Intestine full of the carmine-india ink.

From these observations it seemed that *Heterocope* and *Cyclops* showed a choice of foods while *Diaptomus* and *Nauplii* did not.

The following species were fed for the same length of time on the same culture of algae of the nannotype, with the following results:

Cyclops. Intestine had an occasional alga.
Diaptomus. Intestine full of algae.
Heterocope. Intestine contained a few algae.
Nauplii. Intestine full of algae.

Cyclops have an imperfect filtering arrangement of the mouth appendages, as they obtain only a few of the smaller types of food material. Apparently, they use discrimination. *Diaptomus* do not use any discrimination in choosing their food. They can filter food particles down to a size of one micron. *Heterocope* are the same as *Cyclops* in regard to feeding habits. *Nauplii* seldom show any discrimination, but generally get anything over one micron in diameter.

(c) Rotifers. For the experiments with rotifers, the following genera were used: *Asplanchna*, *Anuraea*, *Conochilus*, *Notholca*, *Polyarthra*, *Synchaeta*, and *Triarthra*.

An examination of the contents of the alimentary canal under natural conditions is as follows:

Asplanchna—All kinds of algae and large zooplanktonts such as rotifers and *Bosmina*.
Anuraea—Slight grayish-yellow mass, one small alga. Green mass with many algae.

Conochilus—Yellow-brown mass with one alga.
Notholca—Same as *Anuraea*.
Polyarthra—Same as *Anuraea*.
Synchaeta—Same as *Anuraea*.
Triarthra—Gray greenish mass with few algae.

Asplanchna is the only rotifer to show large organisms in the food ntents.

Observations were made on the water currents created by the cilia the trochal disc in an india ink suspension. The general directions the water currents are as follows: principal result is a stream from terior to posterior; floating particles striking the cilia of the trochal sc are grasped and transported to the mouth. The cilia do not ork continuously.

Experiments with carmine and india ink suspensions indicated at *Asplanchna* and *Polyarthra* took none of the suspension into the mentary canal. This indicated that they were able to use some scrimination in choosing their food. The other types previously entioned took in both the carmine and the india ink indiscrimi-tely. Algae cultures containing small algae were also used. *As-inchna*, *Conochilus*, and *Polyarthra* did not take any algae into their omachs. The other rotifers were filled with algae.

When larger algae were added to the cultures of rotifers, the follow-g results were obtained:

Anuraea—took smaller algae up to 10 micra.
Asplanchna—took all living plankton over 15 micra (*Cyclotella* and *Bosmina*).
Conochilus—took only smaller algae.
Notholca—took only smallest algae.
Polyarthra—Nannoplankton abundant.
Synchaeta—Nannoplankton abundant.
Triarthra—took nothing over 7 micra.

Asplanchna seems to take only larger food particles. This type ows great discrimination in regard to food. *Polyarthra* and *Cono-lus* show a slight discrimination in regard to food. The other types mined seem to take all small material without discrimination. *planchna* appears to be the only predaceous type examined. The ers take in whatever is in the water regardless of its nature.

b. Marine plankton

Bigelow (84) has summarized the literature on food of marine plankton and gives bibliography. It appears that the marine plankton feeds chiefly on living plants and animals. Some of the more recent and extensive studies are by Lebour (513), who finds that detritus plays an unimportant rôle. In general, digestion proceeds very rapidly and renders necessary special precautions. Direct observation of foodtaking, such as was made by Naumann, appears to be freer from error, wherever it can be carried on. The examination of stomach contents may add knowledge if examinations are made quickly. Much of this work, no doubt, should be done on board a suitable vessel.

V. FOOD OF TAXONOMIC GROUPS

This subject is hardly suitable for treatment here at all. The literature is scattered, the observations frequently lack continuity, and the data represent the food of scattered individuals. However, the following comments are made in the hope that they may aid in the feeding of animals in captivity.

For a general discussion of the physiology of nutrition in the various taxonomic groups, Biedermann's monumental work (83) should be consulted for general facts and literature antedating 1911. All the classes and many orders of the animal kingdom are treated.

The food of the lower invertebrates, especially the aquatic ones, has been touched upon in the preceding pages in connection with the discussion of detritus, plankton, etc. The relations of the smaller soil and terrestrial organisms are probably similar. There remain several groups which should be mentioned because of their suitability for experimental work and their importance in communities. These fall principally in the land arthropods and vertebrates.

1. Land arthropods

Normal growth curves are shown by Yagi (see 226, 993). With the exception of insects, comparatively little is known about the food of land arthropods.

Laloy (507) has discussed the food relations of insects from the standpoint of the different groups, their food and the length of their life histories. There is a relation between the food supply and the duration of the larval period. This period is much shortened when

ne food supply is of a nitrogenous nature, or when the adult has nade some provision for the food supply of the future larva. The rval period is greatly lengthened when the larva has to shift for self and when the food is poor in albuminoids, that is, high in carohydrates. In the forms with a high per cent of the nitrogenous od, the particular kind of nitrogenous food can be replaced by nother food of the same nature. The carbohydrate-eating species ave not this range of food, and the kind of food is limited.

Laloy further states that there is an approximate proportion beveen the rate of development and the amount of nitrogenous food the larva's diet. The greater the proportion of nitrogen, the more ıpid the development.

a. Choice of food. (1). Phytophaga. Grevillius (355) made exnsive food tests with *Euproctis chrysorrhoea* (brown-tail moth), sing a variety of food plants, and summarized the work of others. See 133.) Bachmetjew (50) gave further summary. In fall, the rvae of this species feed on a great variety of plants. In the spring, ıey confine themselves to a much narrower range of food plants. he plants, when analyzed, present a relation between the presence tannin and the feeding. The results were also experimentally sted out by feeding these forms on chickweed (*Stellaria media*) hich has no tannin in its composition. The leaves of this plant ere eaten when smeared with tannin and presented to the young rvae in June. The grass occasionally eaten by the larvae, when ıalysed, showed that there was some tannin in it. Tannin was sumed to have no real nutritive value, in all probability, but apeared to serve the purpose of stimulating the appetite or to be a eans of promoting the mastication or digestion of the food. (54.)

(2) Carnivora. Forbes (301, 303) and Webster (957) have made number of studies of the food of insects, chiefly the so-called carniora, such as Carabidae and Coccinellidae, and found them eating nsiderable plant food, grain pollen, etc., though these groups, pposedly, are carnivorous. It seems that these groups eat selecvely from the food available in much the same way as the Phytoıaga which use various food plants (see p. 110). This makes possie experimentation with food as a variable.

b. Influence of unusual food on larvae. The length of larval stages d life-cycle depends, at least in some cases, upon the food. Above e have compiled experiments in feeding silk worms on different food

plants which are more or less related botanically. Unfortunately, the temperature is not recorded, and it probably modified the differences. (See table 8, p. 110.)

The marked difference in larval life indicated in the work of Hartz is suggestive, though other factors probably had an influence. In the case of the codling moth larva, the time in the apple also differs with the variety of apple (table 9). The development takes longer in Maiden blush apples than in the crabs or Duchess.

TABLE 9

Showing conditions and period of growth of codling moth larvae under approximately constant temperature. (Experiments by C. S. Spooner; from (826))

DESIGNATION*	LARVAE IN APPLE				HATCHING TO EMERGENCE	MEAN TEMP. °C.	KIND OF APPLE
	Into apple, first observation		Out of apple				
					days		
L	9/20	10a	10/13	10a	28.8	16.3	Red Crab
A	9/10	9a	10/3	11a	29.7	21.1	Maiden Blush
A	9/10	9a	9/27	9a	25.0	21.2	Duchess
A	9/10	9a	9/27	9a	25.0	21.2	Red Crab
B	9/10	9a	9/25	2p	23.2	25.9	Duchess
B	9/10	9a	9/25	2p	24.1	25.9	Duchess
B	9/2	8a	9/25	9a	24.0	25.9	Yellow Crab
B	9/20†	10a	9/29	9a	27.0	26.4	Maiden Blush
B	9/10	9a	10/3	2p	32.1	27.2	Maiden Blush

* See p. 531. † Larvae fed in cut on outside the apple for a variable length of time.

2. Aquatic insects (75, 414, 449, 740)

The vast majority of aquatic insects are supposed to be predaceous, but recent studies by Hungerford (414), showing that some of the Hemiptera fed on algae and small bottom animals, cast doubt on the whole question of food habits inferred from form of mouth parts. Further investigation in this general field is desirable.

3. Fishes

The majority of fishes chiefly take animal food. Only a few particularly unimportant marine shore fishes are alga-eaters. Some are scavengers and mud eaters. A few live on plankton, but the majority use other animals smaller than themselves.

Insufficient quantity of food usually results in small size. Herring

ıave been kept in a brackish pond communicating with an estuary vhere they became dwarfed in size. Much of this effect can be ıttributed to insufficient food. Landlocked salmon are usually maller than the same species feeding at sea where food is abundant.

a. Food of young fishes. The work of Forbes (299, 305), in which ıe has shown that the Entomostraca constitute the first food of ɪractically all fresh water fishes, also shows that most species later levelop into the piscivorous type, become insect eaters, general eeders, or mud eaters. Lebour has found the entomostracans to be he first food of marine fishes. (513.)

b. Selection of food. The food preferences of fishes have been exensively studied (304, 306, 309). Pearse (657–659) collected data luring 1914, 1915, and 1916 near Madison, Wisconsin, relating prinarily to the shore fishes of lakes, though the food habits of many rom other habitats were studied. Small fishes were more often exmined than larger, because their food habits were less known. 'ish examined: 1914—383; 1915—111; and 1916—125. Pearse ame to the following generalizations:—Most fish are not indiscriminate feeders, but select specific things from the available food supply. n some cases the power of selecting and rejecting is remarkable (397).

c. Food for fishes in captivity. Atkins states it has been demontrated that the effect of artificial food such as mammal flesh is ither the loss of the power of reproduction or the production of offpring of low vitality. Atlantic salmon fry fed four months on fly ırvae after a few weeks of preparatory feeding on chopped liver rew 27 per cent larger than fishes receiving mammal meat. Another et differed 91 per cent. Mortality was greater in mammal-fed fish. Embody and Gordon (278) give analyses of various artificial and atural trout foods. (42, 542, 586, 640.)

Marine fishes taken as a whole feed on a variety of animals. cott (788, 789) found littoral fishes eating chiefly Crustacea, annelds, and other fishes. Some ate serpent starfishes. Blegvad nds mollusks (101) important in the food of fishes in Danish vaters.

4. Reptiles and Amphibians

Surface (872) has shown that snakes eat a variety of food covering ıe entire series of terrestrial animal groups including birds. The egree to which gastropods were eaten is noteworthy. Aside from ıe toads and frogs very little is known of the food of amphibians.

Toads eat chiefly land arthropods (Kirkland, (477)). Lizards feed largely upon insects.

5. Birds and mammals (37)

Birds select from a wide range of food (129, 302). The latter have been studied extensively under the auspices of the United States Biological Survey, which has issued a series of bulletins on the subject. Herbertson (385a) and McAtee (550) have listed this literature.

Mammals select from a considerable range of food. Their food, even that of the ungulates, has been determined by the examination of stomach contents. It is hardly safe to generalize regarding the food of mammals.

a. Care of mammals and birds in captivity. The wild mice used for experimental work by Johnson (452) were caught alive in box traps and brought to the laboratory, where they were usually placed in wire screen cages of $\frac{1}{4}$-inch mesh. The cages were 25 by 25 by 35 cm. Usually the mice were kept in pairs, but there might be from one to four or more mice in a cage. Most of the mice were kept in the greenhouse, except as they were being used over periods of time in darkroom or attic for activity experiments. Of the greenhouse mice, some were in a section which was artificially heated to room temperature during cold weather, and the others were in a more exposed section subject to outdoor temperatures.

The mice were given cotton and tissue paper for nest-making; and also in some cases wooden nest-boxes of convenient size (10 by 10 by 13 cm.), with a small side-opening for the entrance and exit of the mice, and a removable cover to permit of examination of the nest. Water was supplied usually by the drop method; but in some cases, and particularly in the outdoor cages where freezing was likely, the water was given in open dishes. The principal food for all the mice was whole wheat, but the attempt was made to supply a sufficient variety of food so the mice would not lack any dietary essential. Salted peanuts were given frequently, but sparingly. This writer has found, as did Dice (247), that on a diet of grain without peanuts the mice seem to be lacking something and are inclined to cannibalism. If peanuts are given to excess, however, the mice eat them instead of other food, and may die. Either milk or lettuce was given every few days, to insure a plentiful supply of vitamins.

Wild birds and mammals often become diseased. The best discussions of such problems are by Fox (313) and Hopkinson (410).

CHAPTER V

Soil and the Growth of Food Plants

I. INTRODUCTION

Soil comprises, besides the mineral materials which give it many of its physical properties, a considerable amount of organic matter and a large mass of living things (409, 545, 546, 758, 973). These living things interact with each other and with the organic and inorganic materials of the soil in a manner which has caused the resemblance between soil and an organism to be mentioned. This further makes the phrase metabolism of the soil fully as fitting as "metabolism of the sea" (146, 177, 212, 437, 759, 785).

The fact that organisms, especially plants, tend to modify the soil and overcome soil differences in the course of succession, makes the biological content of soil one of the first considerations in ecological work in the field as well as under experimental conditions. Many animals spend a part of their lives in the soil, while others, a smaller number, rarely leave the soil. In determining the effects of climatic and weather factors upon such organisms, it is necessary to maintain standard, uniform, and—if possible—optimum soil conditions. The greatest difficulty arises in controlling the biological content of the soil. Some of the conditions, of course, cannot be duplicated in experiments. The biological as well as the physical conditions of soil have intimate relations to the size of the root system and vigor of plants which in turn may influence animals under experimental conditions (799).

II. BIOLOGICAL CONTENT OF THE SOIL

1. Roots of plants (146, 953)

Among the most important living things in the soil are the roots of plants. Some striking examples are stated by Weaver (953) as follows:

The native vegetation of semi-arid eastern Washington shows extensive root systems. *Balsamorrhiza sagittata* (Balsam root) is

representative. The strong tap root reaches a depth of 2 meters. Extensive root systems are the rule among grassland species. *Andropogon hallii* (grass), with exceedingly well-branched fibrous roots 2.2 meters deep, is representative of many of the dominants. About ninety per cent of the more important grasses are rooted well below the 65 cm. level, and not a few, such as *Liatris punctata*, extend to depths of 4 to 6 meters.

The great extent of roots in relation to above-ground parts is often very striking (953). *Gleditsia triacanthos* (tree), thirteen weeks after seed-germination, although reaching a height of only 22 cm. produced a remarkably widespread root system that extended well into the second meter of soil. The roots of *Solidago oreophila*, a small species only about 30 cm. high, spread about 60 cm. on all sides of the plant while some penetrated downward to a distance of 70 cm.

Cultivated plants show extensive root systems also (953). Maize (*Zea mays indentata*) has a wonderfully developed root system which occupies rather thoroughly over 5.7 cubic meters of soil. The root system of the sugar beet (*Beta vulgaris*) is likewise very extensive, branching widely and extending downward to a depth of 150 to 180 cm.

The rapidity of root growth is quite as remarkable as root extent. *Spartina cynosuroides* reaches a depth of over 120 cm. at the age of eleven weeks.

Variations in root habit under different climatic conditions are often very pronounced (953). Continued examination of the smaller cereals in fertile silt-loam soils under a wide range of precipitation and soil moisture shows that the root habit varies widely. Under 67 to 80 cm. of precipitation, such as occurs in eastern Kansas and Nebraska, the tops of winter wheat are tall and the roots deep, but the lateral spread is relatively small. But in western Kansas and eastern Colorado, where 40 to 48 cm. of precipitation wet the soil to only 60 to 75 cm. the tops are short, and the roots are shallow but very widely spreading and much more profusely branched. Root habit under an intermediate precipitation of 52 to 60 cm. falls between these extreme types, but is correlated with a medium development of shoots. Two-year-old alfalfa, in fairly moist, deep soil, penetrates with little branching of the tap root to depths of from 300 to 360 cm. Under certain conditions as for example on the Great

Plains, where a subsoil lacking available water prevents downward penetration, so many profusely branched, widely spreading laterals are produced that one would hardly recognize the roots as those of alfalfa.

Pronounced differences in root-development in the same field may also be induced by competition (953). Spring wheat grown at the normal field rate of planting was more deeply rooted when mature than wheat planted four times as thickly. The working levels were 97 and 88 cm. respectively. But in proportion to tops, plants of the thicker stand had much more extensive root systems.

2. *Fungi and microörganisms* (437, 758, 966)

The number of microörganisms, both plant and animal, in the soil is enormous. In some cases it is estimated that 30 grams of fertile soil may contain 30,000,000. A large percent of these belong to the plant group and include bacteria, algae, fungi, and slime molds. The macroörganisms consist of some fungi and slime molds and the larger forms of animal life.

3. *The larger animal inhabitants of the soil*

a. Vertebrates (1001–1005). In California, burrowing rodents constitute one-fourth of the species and one-half of the individuals of the mammals (Grinnell 357). The most widespread, the most abundant, and the most effective burrower in turning over soil is the pocket gopher (*Thomomys*). Its burrows are extensive, of uniform diameter, about 10 to 20 cm. underground, with short side-tunnels. The openings through which the earth was removed to the surface, are plugged from below. In winter snow tunnels are used, and earth is packed into them. From measurements of these earth-plugs, the author estimates 620 gm. of earth per m^2 are brought to the surface each winter in favorable areas.

Among the mammals Hisaw (403) has shown that the mole makes two kinds of runways—surface and deep. In the former the earth is pushed up into a surface ridge, but in the latter the loosened earth is shoved backward to the end of the tunnel, so that these animals move much soil. For work on Russian steppes, see (1001, 1005).

Prairie dogs may go 5 meters into the soil, meanwhile bringing much earth to the surface. Mammals by their activity aerate the substratum, bring new soil to the surface, hasten weathering, bury

vegetable matter, increase porosity of soil and its capacity for holding water and so increase the productivity of the soil for vegetation. Reptiles and toads burrow short distances into the soil with similar effects.

b. *Invertebrates* (130, 142, 143, 602). Insects are sufficiently important in modifying soil to justify a review of the more important soil groups which have been discussed by McColloch and Hayes (559) and also by Cameron (142).

Thysanura and Collembola. Especially abundant in the soil. some Collembola are found at depths of 2 meters or more.

Orthoptera. The Acrididae deposit their eggs in the ground. Many Locustidae and Gryllidae spend much of their life underground

Thysanoptera. Numerous species of thrips are found in and on the ground.

Hemiptera. The Cicadidae and the root-feeding species of Aphididae and Coccidae are intimately associated with the soil.

Lepidoptera. In many cases, only pupation occurs in the soil as among certain species of Notodontidae, Geometrina, Sphingidae, and Noctuidae. Some Noctuidae, especially the cutworms, spend much of the larval period in the ground.

Diptera. The larvae and pupae of a large number of families of Diptera are found in the soil, and especially that rich in organic matter. For example, the Tipulidae, Tabanidae, Lepitidae, Asilidae, Bombyliidae, Therevidae, Dolichopodidae, Mycetophilidae, and Bibionidae are well represented. The parasitic Oestridae leave the host to pupate in the ground.

Coleoptera. The beetles represent one of the largest orders of insects and are especially abundant in and on the ground. The Carabidae, Cicindelidae, Silphidae, and Staphylinidae and others spend their entire life closely associated with the soil. Nearly all of the Scarabaeidae, Elateridae, Lampyridae, and Meloidae, spend the egg, larval, and part of the adult stage in the ground. Numerous species of other families are well represented in the soil fauna (367).

Hymenoptera. The ants, bees, and wasps present many interesting groups of soil-inhabiting insects. The Formicidae, Sphecidae, and many Apidae excavate extensive tunnels, burrows, or cavities in which they store food and rear their young. The adults of many species of Scoliidae burrow through the soil, parasitizing other insects.

The great variety of species and diversity of habits represented by this order make it one of the most important soil groups.

The myriopods, snails, slugs, earthworms, etc., (39, 757, 766) exercise an important influence. The earthworms and their work are especially well known.

III. PHYSICAL AND CHEMICAL CONDITIONS IN SOIL

Lyon and Fippin (546) present a comprehensive outline of the factors of the soil environment.

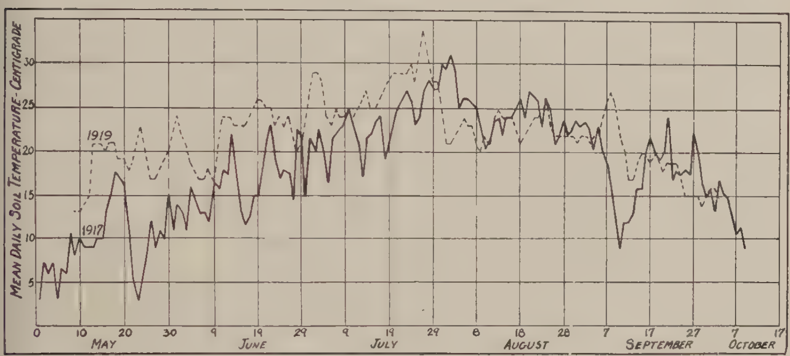


FIG. 51. Graphs showing seasonal variation in soil temperatures during the seasons 1917 and 1919 at Racine, Wisconsin. The graphs are based on the mean daily soil temperature taken at a depth of 10 cm. at two-hour periods. Taken by W. B. Tisdale, Wisconsin Agricultural Experiment Station (courtesy L. R. Jones (459)).

1. *Temperature* (385, 974)

The heat of the soil is from three sources, solar radiation, conduction, and organic decay. It influences the biological, physical, and chemical constituents and it is dependent on many factors, such as specific gravity, specific heat, color, topography, conductivity, air circulation, and water content. Soil temperature differs from air temperature (459) and also differs from season to season, as shown in Figs. 51 and 52. There is a soil temperature "overturn" similar to the overturn in lakes (560).

2. *Air* (146, 177, 367)

The quantity of air varies with soil and is subject to change from time to time. The factors influencing the volume of air are texture,

structure, organic matter, and water. The quality of air differs from that of free air as shown in table 10.

If subterranean animals are to thrive, they require a plentiful supply of air. In general, any factor which tends to keep the texture of the soil loose and open will also favor animals and plants.

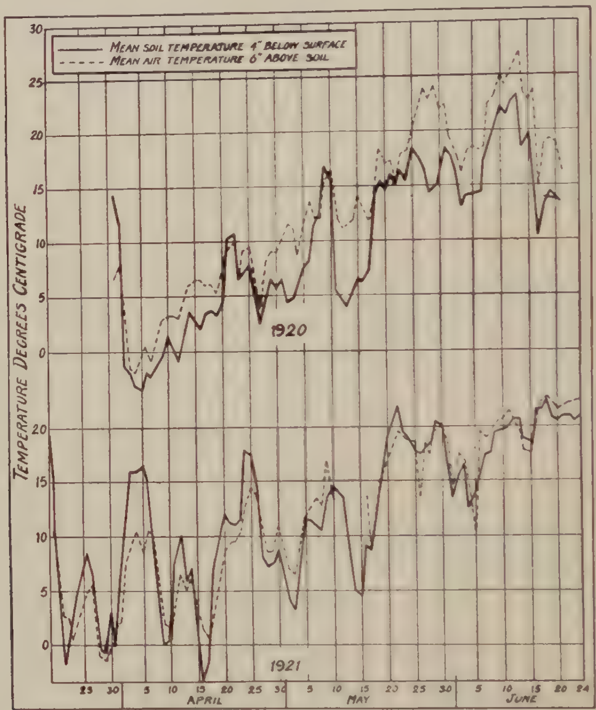


FIG. 52. Graphs showing soil and air temperatures for the spring growing period of 1920 and 1921 at Madison, Wisconsin. The graphs are based on the mean daily temperatures from 15 cm. above the soil surface for air temperatures and 10 cm. below the surface for soil temperatures at two-hour periods. Note the close correlation between air and soil temperature. Data secured by J. G. Dickson. Wisconsin Agricultural Experiment Station (courtesy L. R. Jones (459)).

Deep-rooted plants also mammals and insects open up the soil and admit air, which is advantageous to the healthy development of the roots of plants and to the well-being of soil animals present. Attempts to rear the imagoes of various insects collected from the soil are often unsuccessful in the laboratory for lack of aeration. If the

soil in the breeding cages becomes stale, and its surface bound together so that there is no free access of air, larvae of some species invariably die. Active carabid larvae, for instance, are more susceptible to the injurious effects of this deficiency than dipterous maggots or weevil grubs. If the soil is disturbed at intervals so that air can penetrate easily, better results are obtained (Cameron (142)).

3. Moisture (114, 115, 116, 317, 565, 646)

It is well known that water is the most important agent in determining the degree of fertility of the soil, and is all-important to the vital functions of the plant in its capacity of supplying and carrying plant food to it, but in how far water influences other kinds of terrestrial life beneficially or detrimentally has not been fully ascertained. The character of water which bathes animals during rains

TABLE 10

Differences in quality of air

CHARACTER OF SOIL AIR	CO_2 IN 10,000 PARTS BY WEIGHT
1. Sandy subsoil of forest	38
2. Loamy subsoil of forest	124
3. Surface soil of forest	130
4. Surface soil of vineyard	146
5. Pasture soil	270
6. Rich in humus	543

should be determined with lysimeters (Lyon and Buckman (545)). In the interstices of the soil, water may exist in three distinct forms, which Lyon and Fippen (546, p. 141) explain as follows:

(a) Gravitational water which percolates through the soil under the action of gravity. (b) Capillary water which is held by surface tension against the action of gravity. (c) Hygroscopic moisture, which condenses from the atmosphere laden with moisture on the surface of the particles of an air dry soil.

Cameron (142) discusses the relations of soil animals to water essentially as follows:

Of these three, gravitational water is the most abundant variety, and the one which is destructive of insect life within the confines of the soil. Capillary moisture, on the other hand, keeps the soil just in the right condition

favorable to its fauna, while hygroscopic water, on account of its infinitesimal amount, has practically no significance in questions pertaining to soil animals. The latter experience the most precarious time of their existence during the winter and spring, when, owing to heavy and protracted rain showers, there is an abundance of gravitational water present in the soil, the spaces between the particles being completely filled with water, all air being expelled. Where these conditions are maintained for a fairly long time the larvae and pupae of Coleoptera and Diptera, which undergo their metamorphosis in the soil, are practically killed by suffocation, and, further, the very humid conditions induce liability to attack by fungi, the spores of which are present in all soils. The physical conditions of the soil determine the amount of gravitational water which it will hold; the larger the pore space, and therefore the smaller the particles, the greater the quantity retained. Hence it is that clay soils do not allow of its percolating so quickly as a loose, sandy soil, and this, added to the fact that the capillary capacity of clay is much greater than that of any other kind of soil, gives the former its generally moist appearance. Thus it will be readily understood why a clay soil is generally shunned by the more active insects, besides its impenetrability, it imbides and retains too much water.

4. Hydrogen ions (46, 47, 328, 334, 335, 336, 467, 766, 878, 925, 971)

Both electrometric and colorimetric methods have been used, and results approximately agreed. Soils were found with a pH of 4.4 to 8.6. (See Chapter XIX, especially pp. 485–500.)

The various sources of error in the methods of determining the H-ion concentration are: the dilution of the soil extract, loss of carbon dioxide, and the difficulty of comparing a clear and a turbid solution. There has been little study of soil reaction from the standpoint of animals. Presumably the water in very acid soils would be more likely to injure small animals during heavy rains, than in alkaline soils.

IV. FOOD OF SOIL ANIMALS

The food of the smaller subterranean animals consists principally of decaying organic matter and micro- and macroörganisms (130, 602). All of these occur in varying quantities in practically all soils. Decaying organic matter is probably the most important, since it not only furnishes food for a large number of insects, but also influences the number of micro- and macroörganisms. The amount of organic matter present varies greatly with different soils, a conservative average being from 2 to 3 per cent. The fertilizing of soil increases the microörganisms and thereby the life in general.

V. FOOD PLANTS

1. General consideration

Under experimental conditions food plants for animals deserve onsideration. The phytophagus animals most likely to be experiaented upon are insects. Few are restricted to one food plant. 'olsom (296) states that the migratory locust feeds on upward of 50 plants. The common white caterpillar (*Diacrisia virginica*) nd the tarnished plant bug (*Lygus pratensis*) feed on all sorts of herbge growing in sunlight. Evidently their distribution is not governed y food.

The evidence of food effects cited in Chapter IV shows how imporant it is to select a good food plant from the standpoint of the insect efore beginning experimentation. The guiding principles, if they re to be had without experimentation, are suggested by Brues in apers (123–125) and other writers cited by him. The essential acts are as follows: A few insects feed upon a single species. In some ases the larvae on hatching feed on the plant on which they happen o be (one of several utilized by the species) and cannot be induced to hange to another, though they eat it if it is presented at the beginning. Others change readily from one plant to another in mid-larval ife, where such changes are forced. "Food plant sub-species" have sometimes been recognized, that is, groups within a species which differing only in that they use different food plants. These facts may account for the failure of experimenters to secure any food that a lot of injudiciously collected insects will eat. Changing food plants is an especially good subject for study. A kind of memory of food would appear to be carried by the adults arising from larvae fed on an unusual plant as in some cases they select it for egg-laying. Food selection investigations should be carried on under conditions of climate simulation and control, as the results are evidently modified by external conditions. Some insects feed upon any grass or sedge; others on almost any herb. Occasionally an experimenter will find that his insects will not feed upon any of the food plants he secures. There have been changes in the plants eaten by various insects during the destruction of original biota and the agricultural dispersal of insects of all kinds into new conditions.

Some insects feed upon fungi and algae growing in moist places.

For example the Tetrigidae successfully bred by Dr. Nabours (personal communication) at Manhattan, Kansas, feed on algae and lichens. He bred *Apotettix eurycephalus* Han. from Mexico and *Paratettix texanus* Han. from Texas. They were fed on filamentous algae over a period of years under ordinary greenhouse conditions. Species native near Chicago and Manhattan were not successfully bred in greenhouse conditions. The cultures failed, whether due to food, temperature, or absence of ultra-violet is uncertain. It affords a good example of the importance of going south for material to be bred in an unconditioned greenhouse.

2. Distribution in relation to food plants

There are very few phytophaga that are confined to single plants and accordingly their distribution is generally governed by other factors. (Metcalf (594)). If one makes a list of the food plants of an insect in its original climatic conditions he usually finds that they are some of the predominant trees or other plants of some plant association. This fact may sometimes prove very useful in locating the original habitat of a species which has dispersed widely under agricultural conditions. Some agricultural pests have followed their food plants nearly throughout the world. The codling moth is an example (Simpson (844)). These facts have important bearing on the interpretation of climatic relations.

3. Relations of food plants to animals under experimentation

The plants which are necessarily used as food for insects of agricultural importance will rarely come to maturity under the conditions imposed upon animals. In any large series of experiments they clearly will not under all the conditions imposed. The experimenter accordingly must decide whether he wishes to supply uniform food to all experiments throughout the period of experimentation, carry the insects through the food series presented by the normal development of the plant, or otherwise vary the food. In most cases where animals—usually insects—are kept in confinement under experimental conditions in pots in reduced light, etc., the food is different from that which the animals normally have in nature. The food plant then becomes an experimental factor.

4. Effects of variations of food plant upon animals

Unfortunately, little or nothing is known of the effects upon animals of the food differences induced in plants under experimental conditions. Such general facts as have come to our attention are noted in Chapter IV. These are concerned with differences in the age of plants, differences in kinds of plants, plants at different seasons and in different localities. The work is chiefly European and concerned with species not generally distributed in the United States and Canada.

In the succeeding paragraphs, we call attention to the manner in which plants vary in relation to conditions. Special attention is called to the fact that different plants respond differently.

5. Physiology of plants as affecting their use as animal food (727)

Plant mortality is commonly greatest among the young individuals due to over-crowding, disease, drought, and unfavorable aerial temperature and humidity. In the very young stages, however, plants are not likely to die from lack of nutrition, as a large reserve of food material is carried in the seeds.

Relative to the foodstorage process of plants from a chemical viewpoint, Nightingale (624) has stated the following general principles:

Nitrates may be stored by the plant within itself until the proper conditions rise for synthesis to other forms of nitrogen. The presence or absence of nitrates within plants does not necessarily affect the type of growth. Proteolysis to nitrates did not occur in tomato plants even after 284 hours of continuous darkness. Data are presented which indicate that hemicellulose is utilized by the plant as a source of sugar, but there is apparently little degradation of hemicellulose unless there is a marked depletion of starches and dextrins. The following four classes, based upon those of Kraus and Kraybill (see 624) are suggested:

1. Though there be present an abundance of amino acids and other forms of soluble nitrogen, not necessarily including nitrates, yet without an available carbohydrate supply[1] there may be decomposition of protein nitrogen. If present in sufficient amount, vegetation is weakened, and the plants are nonfruitful.

[1] It would seem that sugars, starches and dextrins are more intimately associated with the food metabolism of plants than is hemicellulose, but data sufficient for conclusions are lacking.

2. An abundance of amino acids and other forms of soluble nitrogen, not necessarily including nitrates, coupled with an available carbohydrate supply, accompanies increased vegetation as compared to No. 1, barreness and sterility. Concomittantly, as nitrate free soluble nitrogen is present in abundance, a large proportion of the assimilated nitrogen is not accumulated as protein.

3. A relative decrease of amino acids and other forms of soluble nitrogen, not necessarily including nitrates, makes for an accumulation of carbohydrates and also for fruitfulness, fertility and lessened vegetation as compared to No. 2. There may also be an accumulation of much of the assimilated nitrogen as protein.

4. A further reduction of amino acids and other forms of soluble nitrogen, not necessarily including nitrates, accompanied by an increase of carbohydrates makes for an accumulation of the assimilated nitrogen as protein, and for a supression both of vegetation and fruitfulness when compared to No. 3.

Note: In each of the four preceding classes it is assumed that plant foods, (that is products synthesized within the plant) are not limited except as indicated. A mineral nutrient, for example potassium nitrate, is not classed as a plant food, while amino acids, sugars, proteins, etc. are so considered. Also, it is assumed that nitrates are not present in sufficient amounts or in such salt combinations as to be toxic to the plant.

Throughout this work the relative amount and not the total amount of plant foods was associated with type of growth responses. The total amount of plant foods present was correlated only with total amount of growth made.

1. When there is no external supply of nitrogen or opportunity for carbohydrate synthesis and reserve carbohydrates are depleted there is decomposition of protein and an increase in amino acids, amide and proteose nitrogen. If carried far enough, as stated above, this condition results in a weakly vegetative growth.[2]

2. When protein is decreased further, as compared to 1, without an available supply of carbohydrates, death ensues. Associated with the approach of death is an enormous increase of an as yet undetermined fraction of soluble nitrogen. This fraction may be comparable to a "ureide fraction" secured by Chibnall.

3. Under the conditions described in 2, if a supply of carbohydrates is made available to the plant before death of much tissue there is eventually a decrease of this ureide (?) fraction and also a decrease in amino, amide and proteose with an increase in protein nitrogen. Coupled with the accumulation of protein nitrogen there is an increase in carbohydrates.[3]

[2] Growth as here used means production of new tissue as demonstrated by an increase in volume of the plant even though such may involve a loss in dry weight.

[3] From the available chemical data it is impossible to say whether the accumulation of carbohydrates occurred simultaneously with or followed the accumulation of protein.

4. In the case of tomatoes, light within the limits of a six-hour day did not ppear markedly to limit the assimilation of nitrates, providing there was esent an available supply of carbohydrates.

Since many animals require food plants, the effects of experimental nditions upon plants require careful consideration. It is now iown that the various conditions imposed upon plants in varying e surroundings for animals affect their properties as food.

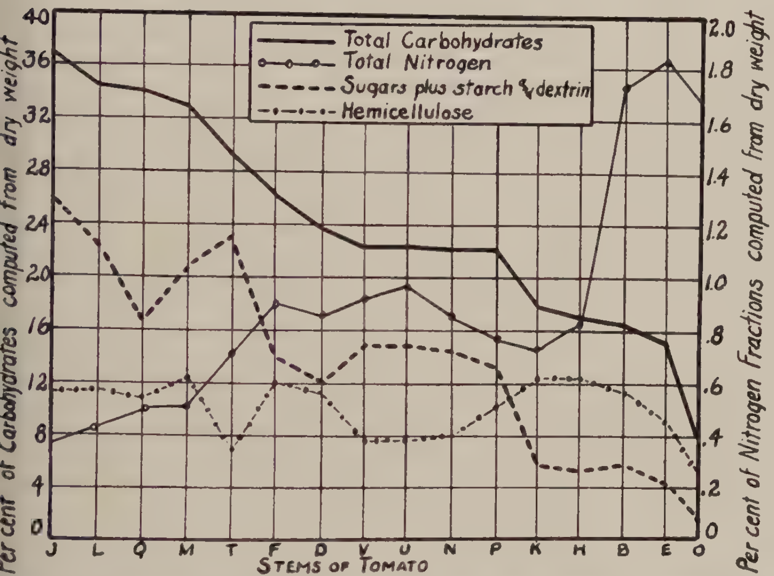


FIG. 53. Showing the effect of light and other conditions on plants (after ghtingale (624)). *J*, long day minus nitrogen; *L*, short day to long day, twelve-hour greenhouse day light, do.; *M*, normal greenhouse light, do., normal light; *F*, short day to long day plus nitrogen; *D*, long and nitrogen; darkness to light; *U*, light to darkness; *N*, light to dark; *P*, full light to ort day; *K*, long day to short day; *H*, short day minus nitrogen, etc. The der should consult the original for an understanding of the experimental nditions.

a. Length of day. The effects of length of day on the quality of nts is marked, as shown by the quotations from Nightingale and ures 53 and 54:

1. Tomato plants grown for three weeks, with fourteen hours illumination day and with no nitrogen in the nutrient solution, made little growth, re yellow in color, stunted and unfruitful. After these same plants were

grown for four weeks with only six hours illumination per day, and with no nitrogen in the nutrient solution, they elongated rapidly, turned dark green in color and produced many blossoms. Associated with the increased growth was a decrease in percentage of carbohydrates and an increase in percentage of nitrogen.

2. Tomato plants grown for three weeks with fourteen hours illumination per day and with nitrates in the nutrient solution were vigorously vegetative and fruitful. After these same plants were grown for four weeks with only six hours illumination per day and with nitrates in the nutrient solution, they grew less rapidly than before, and were unfruitful. Associated with the decreased growth was a decrease in percentage of carbohydrates and an increase in percentage of nitrogen.

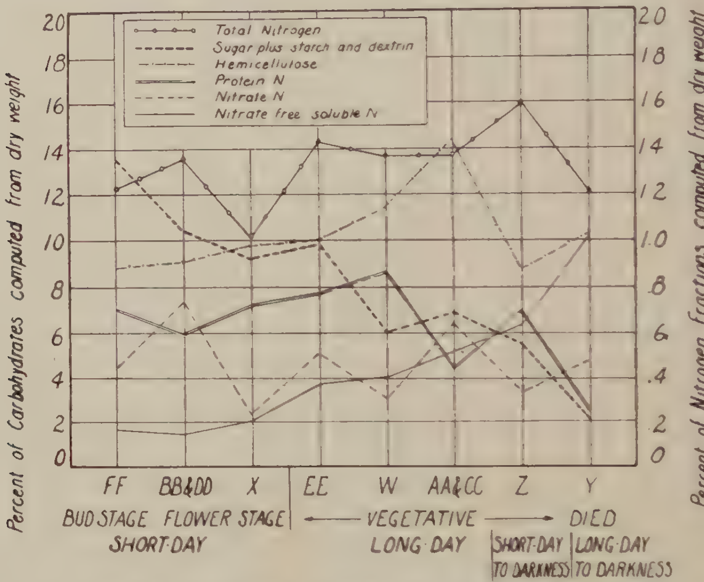


FIG. 54. Showing the effect of light and other conditions on the quality of Salvia plants (after Nightingale).

3. Tomato plants grown for three weeks with six hours of illumination per day and with no nitrogen in the nutrient solution were dark green in color, moderately vegetative, and produced many blossoms. After these same plants were grown for four weeks with fourteen hours illumination per day and with no nitrogen in the nutrient solution, growth decreased very much, the plants turned yellow in color, and ceased to blossom. Associated with the decreased growth was an increase in percentage of carbohydrates and a decrease in percentage of nitrogen.

4. Tomato plants grown for three weeks with six hours of illumination per ay and with nitrates in the nutrient solution were weakly vegetative and nfruitful. After these same plants were grown for four weeks with fourteen ours illumination per day, growth increased very much and the plants became ruitful. Associated with the increased growth and fruitfulness was an in- rease in percentage of carbohydrates and a decrease in percentage of nitrogen.

5. Salvia, unlike tomato, was apparently limited in the assimilation of itrates by a seven hour day, even though there was present an available ipply of carbohydrates.

6. In addition to salvia, buckwheat, soybeans, and radish were limited in ie synthesis of nitrates to other forms of nitrogen by a seven hour day. lso associated with relatively little assimilation of nitrates was an accumula- on of carbohydrates within these plants when subjected to a short photo- eriod.

7. Carbohydrates accumulated in the short-day plants, presumably be- ause there was relatively little utilization of them in the synthesis of nitrates o other forms of nitrogen.

8. The rapid growth of high carbohydrate short-day salvia plants, when ıbjected to a period of complete darkness, was associated not only with a loss f carbohydrates presumably chiefly through respiration, but with an increase ı the nitrate free soluble nitrogen fraction. Coupled with the increase of itrate free soluble nitrogen there was a decrease in protein, probably due to espiration of it.

9. On the other hand, rapid growth of high carbohydrate short-day salvia lants, when transferred to long-day conditions, was also associated with a loss f carbohydrates. When salvia plants are subjected to long-day conditions iere is a more rapid assimilation of nitrates and a greater accumulation of itrate free soluble nitrogen than when they are subjected to short-day condi- ons. Accordingly, it may be inferred that associated with assimilation of itrates there would be utilization of and therefore a decrease of carbohydrates.

10. Data are given which indicate that the growth responses and the asso- iated relationship of carbohydrates to nitrogen in roots are unlike the growth esponse and associated relationship of carbohydrates to nitrogen in the tops f the same plants. In general, the leaves and stems of the same plants are milar in this respect.

11. In all cases the root system of weakly vegetative high carbohydrate lants was proportionally much more extensive that the root system of plants w in carbohydrates and vigorously vegetative.

12. Out of a lot of 700 very uniform tomato seedlings, 470 plants were chosen or immediate analysis of the whole plants. The remainder of the plants were iven a nutrient culture containing no nitrogen. After a period of about six eeks these whole plants were analyzed for total nitrogen and there was an icrease in absolute amount of it.

13. The plants which were subjected to a short photoperiod gained more in osolute amount of nitrogen than did the plants which were subjected to a long hotoperiod.

b. Effect of quality of light. Different wave lengths have different influences upon the growth and composition of food plants (fig. 55). Popp (682) has studied the effect of different qualities and quantities of light. Table 11 gives his results on Sudan grass and shows the chemical composition of the plants grown under the various ray filters at the Thompson Institute.

c. Effect of temperature Walster, working on barley, found that high temperature (20°C.) leaves contain about twice as much nitrogen as low temperature leaves. High temperature leaves contain nearly twice the percentage of alcohol soluble phosphorus. Low

TABLE 11

Analyses of Sudan grass, entire tops of plants (92 days from planting; all in houses 92 days)

HOUSE	TOTAL WEIGHT OF TOPS	WEIGHT PER PLANT	MOISTURE	NITROGEN —GREEN	ACID-HYDROLYZABLE MATERIAL—GREEN	SUCROSE —GREEN	DEXTROSE —GREEN	TOTAL CARBOHYDRATES —GREEN
1	299.0	18.7	71.35	0.29	7.88	0.92	0.48	9.28
2	255.3	21.3	74.77	0.28	6.99	1.17	0.57	8.73
3	263.5	20.3	72.30	0.22	6.94	0.88	0.64	8.46
4	294.3	17.3	78.83	0.26	3.69	0.93	0.65	5.27
5	616 0	20.5	81.70	0.29	4.00	0.99	0 54	5 53

temperature leaves contain a high amount of polysaccharides, but the difference is small. The average proportion of frame work is greater in low temperature plants. Stephens and Higgins (568, 862) found that temperature influences the quality of sweet corn.

The effect of soil temperature upon the growth of corn is shown in figure 56 (Jones and others (459)). Similar experiments upon wheat showed the best growth at the lower temperatures (fig. 57).

d. Effect of soil and food supply. Soil has marked effect upon the vigor and size of plants. Its cultivation, aeration, etc., also have an influence.

Fig. 55. (1) Sudan grass from houses 1 to 5 (Thompson Institute), seventy-six days from time of planting; plants had been in houses seventy-six days. Table 11. (2) Sunflowers from houses 1 to 5, eighty days from time of planting; when plants had been in houses seventy-six days. (3) Carrots from houses 1 to 5, 143 days from time of planting; when plants had been in houses 139 days. After Popp (682); (courtesy of the Boyce Thompson Institute).


1
HOUSE I
HOUSE 2
NOV 10
HOUSE 3
Plants 76 days old. In houses 76 days
HOUSE 4
HOUSE 5
2
HOUSE I
HOUSE 2
NOV 10
HOUSE 3
Plants 80 days old. In houses 76 days
HOUSE 4
HOUSE 5
3
HOUSE I
JAN 12
HOUSE 2
Plants 143 days old. In houses 139 days
HOUSE 3
HOUSE 4
HOUSE 5

FIG. 55

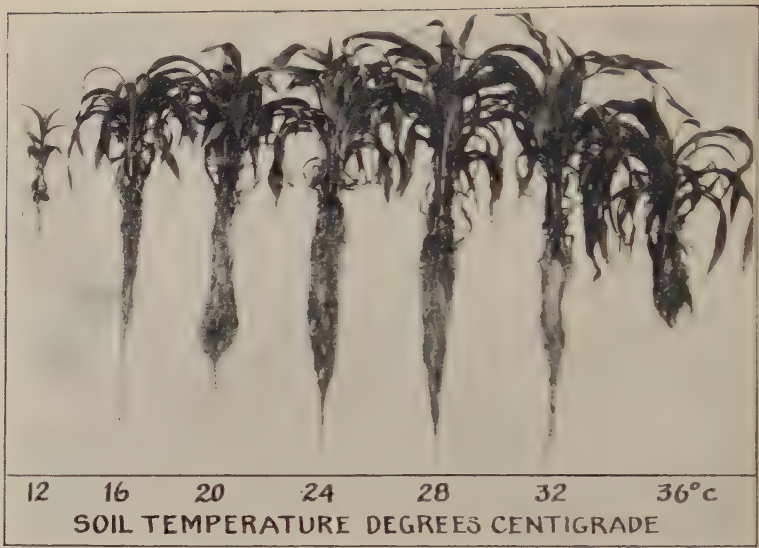


Fig. 56. The influence of soil temperature upon the development of corn plants. Note the strong root systems at 24° to 28°C. Compare with the wheat plants (fig. 57). Wisconsin Agricultural Experiment Station (courtesy L. R. Jones (459)).

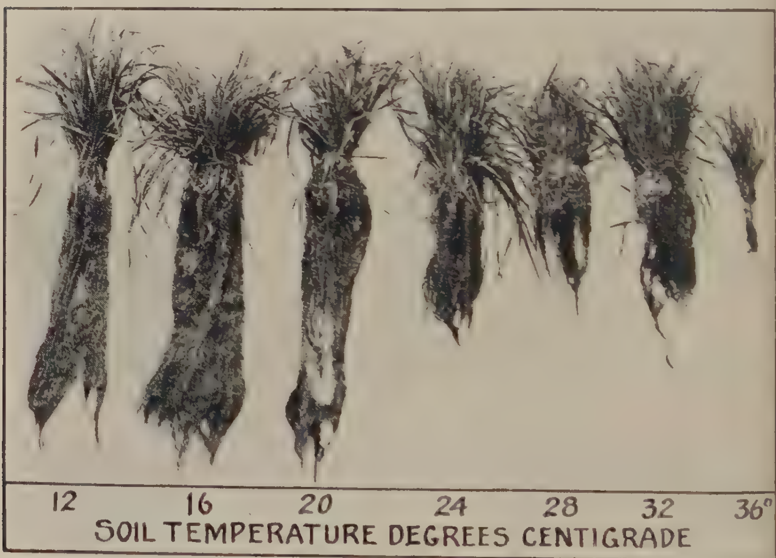


Fig. 57. The influence of soil temperature upon the development of winter wheat plants. Note the strong root systems developed at the low soil temperatures. These plants matured many large heads whereas those grown at the high soil temperatures did not head. Wisconsin Agricultural Experiment Station (courtesy L. R. Jones (459)).

As soil is the source of inorganic foods for plants, its chemical and ıysical properties must be considered. Walster (939) found that gh nitrogen supply at 20°C. gives high soluble nitrogen in leaf, w soluble carbohydrates, accompanied by excessive vegetation ıd little culm. High nitrogen supply in nutrient solution at 15°C ves low soluble nitrogen in leaf, high soluble carbohydrates, with ɔrmal vegetation and normal culm. The amount of organic sul-ıur in alfalfa differs in different parts of the United States.

e. Effect of repeated plantings in culture cages. In the work on inch bugs carried on for the Illinois Natural History Survey, ıdan grass was finally used with much better results than wheat it grew continuously and did not require replanting. Certain periments requiring special care were made with fresh pieces of ıdan grass grown under as nearly uniform conditions as possible d inserted into the experimental tubes each day. Wheat was used first but was discontinued because it had to be replanted every w days and the soil soon became foul with decaying seed and mould ew freely. Bad results have commonly accrued from repeated ınting in the same soil.

Methods of renovating soils have been investigated by Livingston d others (519, 524). In experiments (524, p. 33) in which wheat ıs planted three successive times in the same soil, a decreased ɔwth was shown for the latter plantings. In another experiment . 32) carbon black was added to a pure soil, with a resulting increase growth. Some replantings in quartz sand are discussed (p. 34). second planting gave a growth less than half that of the first plant-g, but almost as much as the first when ferric hydrate was added. ıese conditions formerly credited to root secretions are now held be due to bad aeration and accumulated organic matter coupled th bacterial action. Livingston's results also show the effects of e and soil conditions on the chemical composition of food plants.

6. *Fruits and woody plants*

One of the greatest difficulties in feeding animals upon woody ınts in the laboratory is the large size of the plants. This is a cidedly limiting factor in all cases where the larvae feed in the ıit, and the experimenter has recourse to the smallest dwarfs he

can secure.[4] The results on picked fruit are markedly different from those on growing fruit. For insects feeding on the leaves and twigs, an abundant supply of seedlings of small size is the most likely solution, and advice must be sought from persons with knowledge of proper seed-planting methods and of sources of suitable seed. Field space for growing them must be available (51).

7. The maintenance of a constant quality and quantity of food in experiments

It is very important that the food be maintained constant in climatic-simulation experiments in which the effect of climate is to be separated from the effect of food, including changes in the food plant with advance of the season and approaching maturity. Of course, it is highly desirable from an ecological viewpoint to get the combined effect of any set of conditions directly on the animal and indirectly on it through the effect of the same conditions on the food supplied by the plant upon which it feeds. It is almost equally important to avoid misinterpretation by doing a double series of experiments, one with the possibility of a double effect and another with a constant quality and quantity of food and with the direct results of physical condition thus segregated.

A constant food can usually be approximated as follows: (a) The simplest way is to supply a new plant daily in its soil and pot, but this usually is difficult or impracticable as the small insects and young stages can not be transferred from one plant to another and should not be handled. In the case of the chinch bug—in addition to the mechanical difficulties—there is a strong tendency for the insects to go below the surface of the soil close to the stem. (b) Repeated plantings of quick-growing seeds afford a good solution except for the fact of soil deterioration noted above. (c) Cut plants may be supplied regularly to many insects, and if the feeding is frequent the effects of wilting and drying in the low humidity experiments has to be reduced to a minimum. The woody plants present similar but even greater difficulties.

[4] Dwarf apple trees are obtained by grafting the desired scions on French wild apple roots. The trees bear when they are only a few feet high and the fruit has the characters of the original source of the scion. Of course, sprouts forming from the root will bear the French apples.

McColloch (558) has made progress in the direction of uniform
od (fig. 58) by growing plants in a nutrient solution.

In his Hessian fly investigations, wheat was planted in soil or sand
d allowed to grow to a height of 5 to 7 cm. The plants were
en removed from the soil, the roots thoroughly washed to remove

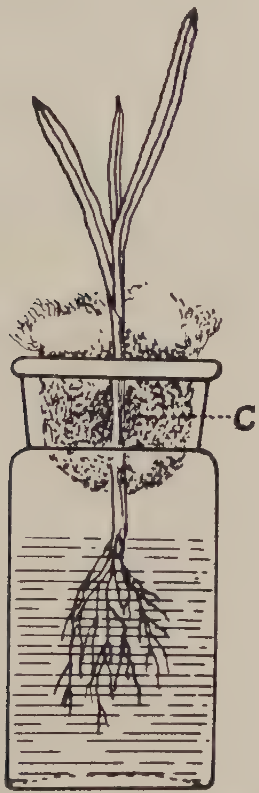


FIG. 58. Water culture bottle used by McColloch (558) who confined small
ects in the cotton cell (*C*).

soil particles, and then placed in wide-mouth (200 cc.) bottles,
ntaining about 150 cc. of the water culture (fig. 58). One plant
s placed in each bottle. The roots were immersed in the liquid
d the stalk was kept in position against one side of the neck of the
ttle with a cotton stopper. The liquid plant food used was that
own as Pfeffer's solution, prepared as follows:

Calcium nitrate	4 grams
Potassium nitrate	1 gram
Magnesium sulphate	1 gram
Potassium dihydrogen phosphate	1 gram
Potassium chloride	0.5 gram
Ferric chloride	Trace
Distilled water	3 to 7 liters*

* McColloch states that he has found that five liters is best for the work under consideration.

The plants grew well but at times difficulty was encountered by a growth of algae in the liquid. This was largely overcome by painting the bottles black. Usually the plants lived long enough for the purposes of his experiments, without changing the liquid. When the experiments were prolonged the solution was changed.

By using this method, he followed the life history of the Hessian fly from oviposition to the formation of the puparium. The plants were handled conveniently and the various stages studied with greater ease and exactness than when the plants were grown in the soil. When necessary, the plants could be removed from the bottle and placed under a binocular for close study. By carefully shaving the epidermis of the leaf sheath, it was possible to keep larvae under observation at all times. As larvae increased in size they could readily be seen through the neck of the bottle.

This method proved so successful in the Hessian fly work that it was adopted by McColloch for the study of a number of other insects infesting cereal crops. He grew wheat, oats, rye, barley, corn, and many of the sorghums in Pfeffer's solution in connection with studies of the chinch bug (*Blissus leucopterus* Say), green bug (*Toxoptera graminum* Rond) and corn leaf aphis (*Aphis maidis* Fitch).

Certain modifications in the method of handling the plants were found necessary for these insects. In order to confine them on the stalks of plants, a small cell was formed in one side of the cotton stopper (fig. 58). The cotton fibers served as effective barriers in holding the insects and exact data could be obtained on molting and length of instars, and, in the case of aphids, on the number of young produced. This method was also used to study certain phases of activity of several parasites of the Hessian fly puparium. The parasites were confined in the cells with plants containing "flaxseed" in their natural position and the behavior and methods of oviposition

f the parasites were easily observed. Good results were obtained ι confining leaf-feeding insects on leaves by inverting another bottle ver the plant or by lowering the plant so as to bring a part of the ·af into the cell.

VI. THE CONTROL OF SOIL CONDITION

The duplication of soil temperature for observation has been ac- omplished by McColloch (557) by means of a cement cave. The oor of this cave is 8 feet below the surface of the ground and the roof feet below the surface. The floor space is 5 by 7 feet. The walls, oof, and floor are 6 inches thick, and the roof is reinforced. The ntrance is through a manhole at one corner with an iron ladder ·ading down to the floor. The advantage of the manhole type f entrance is that it does not cause much change of temperature 'hen opened. Insects appear to thrive under the conditions in this ave during the winter, and the mortality is very low. McColloch ad been attempting to carry corn ear-worm pupae through the winter or several years, but always with negative results because the mor- ılity would be from 75 to 100 per cent. With the material kept in ıe cave, less than 25 per cent died. The behavior of many of the ısects kept in the cave was checked with field observations to de- ·rmine what variations, if any, occurred. Corn ear-worm larvae, laced in the cave early in October, pupated at the same time as did ıose in a check kept in the field insectary. In the spring, the adults nerged during June which is the normal time of emergence in the ·ld. Grasshopper eggs hatched in the cave at the same time that ggs were hatching in the field. All white grub and wireworm ·arings of Kansas Experimental Station have been successfully ırried on in this cave.

1. *Temperature and aeration*

In connection with plant-disease work a system of temperature ontrol for soil has been developed at the University of Wisconsin y L. R. Jones and his colleagues (459). The apparatus is shown figures 59 and 60. Water is maintained at a constant temperature y means of a thermostat. The water-tight pots in which the plants e grown are surrounded by the constant-temperature water. There no provision for cooling below the temperature of running water,

and presumably the lower temperature experiments reported were carried on when the water was cold. The Taylor thermostats are well adapted to insertion into the water, and intermediate air thermostats may be made to admit a mixture of hot and cold water of any desired temperature. There should probably be some method

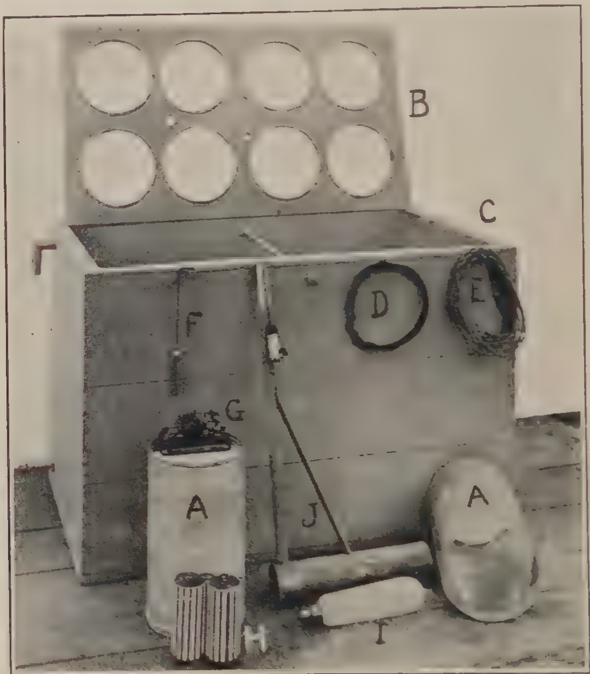


FIG. 59. Wisconsin soil temperature tank and equipment. The cans (*A*, *A*) are suspended from the rigid cover (*B*) in the water tank (*C*). The electrical equipment includes heavily insulated duplex wire (*D*) for heating current, lighter electrical fixture wire (*E*) for battery current, thermostat (*F*), pony telegraph relay (*G*), dry cells (*H*) or storage battery, Edison partial vacuum heating unit (*I*). This heating unit is inclosed in a water-tight copper case (*J*). Wisconsin Agricultural Experiment Station (courtesy L. R. Jones. (459)).

of aerating the soil for the soil animals as well as for the plants. Inverted pots in the center, or coarse materials strewn over the bottom of the cans would be in accord with ordinary practice. Whether a very slow leak from a compressed air line in a perforated tube would

e effective is not clear, but it would increase the contact of the soil vith air.

The water-controlled soil temperature and moisture apparatus or experiments on tiger beetles as shown in figure 61 (813), gave vertical temperature gradient and a difference in humidity, the atter by manual operation.

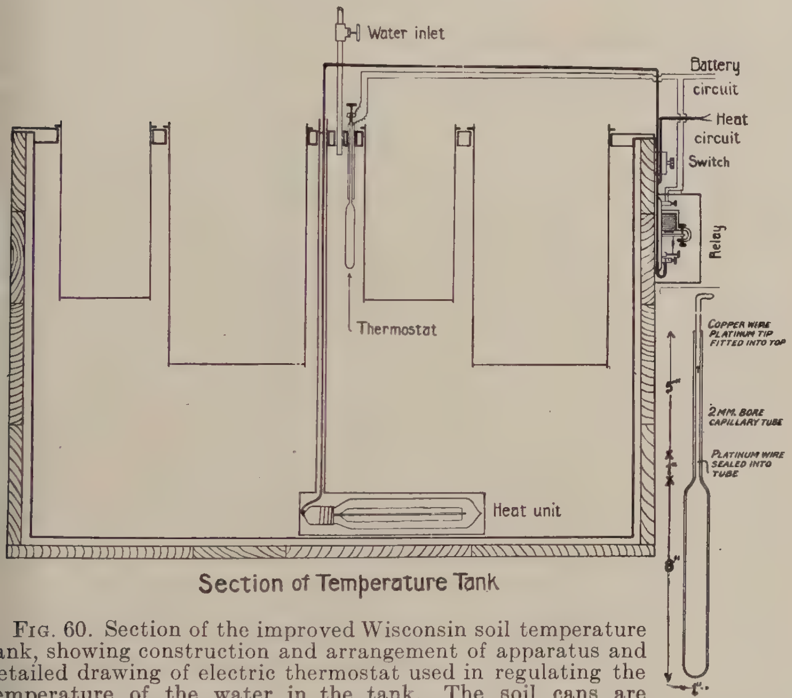


FIG. 60. Section of the improved Wisconsin soil temperature ank, showing construction and arrangement of apparatus and etailed drawing of electric thermostat used in regulating the emperature of the water in the tank. The soil cans are ispended in the water from the rigid cover. Water for cooling d filling the tank is run in through the water inlet. The alternating 110-volt eating current is carried through heavy wires from a switch to the relay and ence to the heating unit which is enclosed in a water-tight copper tube. he direct current operating the relay is carried from storage batteries through e thermostat (shown in detail in insert) to the magnet on the relay. The ermostat consists of a thin glass bulb blown on the 2 mm. capillary tube and platinum wire sealed into the tube one inch above the bulb. The glass tube filled with mercury after which the copper wire with platinum point is adsted in the top of the tube. Wisconsin Agricultural Experiment Station ourtesy L. R. Jones).

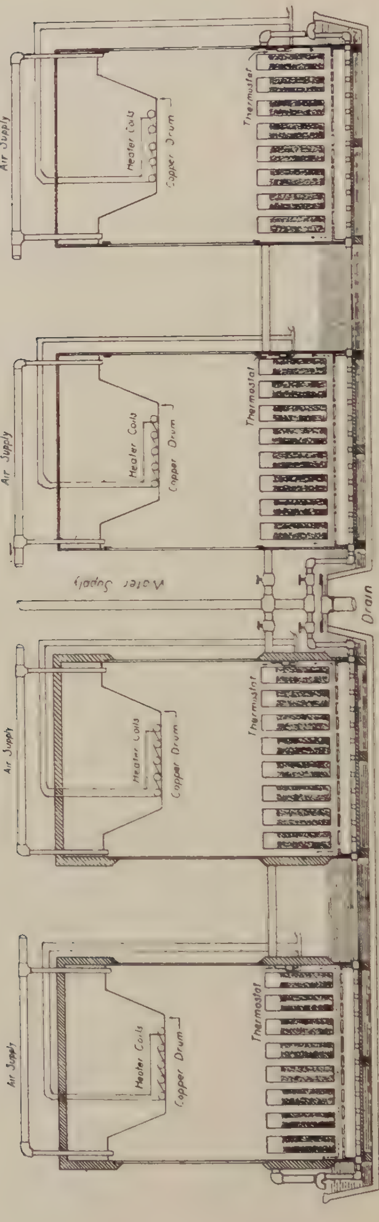


FIG. 61. A set of four light chambers for soil animals (813). Screen-bottom trays holding straight tubes for tiger beetle larvae are shown. The tank may be surrounded with water and cold water coils run beneath the screen trays. The heating is from above (when desired) and a copper drum distributes the heat.

2. *Moisture*

Soil moisture may be maintained by placing a porous clay capsule Livingston (522, 526)) filled with water in the soil and connecting t with a reservoir. The reservoir may be raised or lowered to reguate the amount of moisture. Automatic regulation could be mainained for soils low in moisture by placing some hygroscopic substance uch as wood in contact with the soil. If the moisture content is reat, difficulties would be encountered but these would not be inuperable. Soil moisture has also been maintained by daily weighngs. This method was used by Cook in his work on cut-worms.

Livingston and Ohga (526) also determined soil moisture with orcelain points. At the present stage of development of this method he most satisfactory soil points are little hollow pieces of porous porelain, each consisting of a cylindrical neck and a conical tip. The vall is about 3 mm. thick. The cylindrical part is about 1.4 cm. in liameter outside and 2.5 cm. long. The conical part is 5 cm. long, apering to a point at the closed end. The whole external surface is vater-proofed excepting a conical zone or band 2 cm. wide, its upper nargin being 3 cm. from the cone point. Across the outer surface of he uncoated zone, water is absorbed from the soil, into and against vhich the surface is firmly pressed. The dry piece is applied to the oil, and a reading is simply the increase in weight due to absorption f water during the period of exposure. If the period is of proper ength, the porous porcelain retains throughout the period its ability o absorb water rapidly, so rapidly that the amount absorbed may be aken as a measure of the rate at which water may be supplied from he soil. The basis of the method is simply that, if the absorbent urface takes up water as rapidly as the liquid reaches it, then the ate of water absorption must be determined only by influences acting in the soil, outside of the instrument itself, and the amount aborbed during a period may be taken as a measure of the amount eaching the absorbent surface from the soil during the period. For oils that are obviously wet (to the touch, etc.) the period of exposure nay be short, but for soils whose water-supplying power is relatively ow (less than perhaps two grams per hour per soil point) a 1-hour eriod is not too long.

CHAPTER VI

Dormancy and Other Quiescent States

I. INTRODUCTION

The purpose of this chapter is to point out certain guiding principles and working hypotheses for the investigation of quiescent states, indicated by the work of several recent investigators. These principles and hypotheses have to do with the physiology of quiescence.

Until recently, the general subject of quiescent states has been without adequate working hypotheses or guiding principles. Under the term quiescence are included hibernation, estivation or cessation of activity at any time of the year. The term hibernation is used to cover overwintering in a state of inactivity without feeding. It is occasionally applied to eggs and other quiescent stages while passing the winter. Estivation is applied in a similar manner to passing the summer in an inactive state.

Terms used in connection with quiescent states, as a rule, have been applied very loosely. Dormancy is a term which may well be used, as it is commonly employed with reference to seeds, with a considerable degree of definiteness. Accordingly, in this book, the term dormancy is used in cases where activity or development, insofar as causal observation is concerned, is spontaneously arrested. Cases in which activity or development is stopped because of unfavorable surroundings, only to be taken up again under suitable conditions, are regarded as not coming under this head. They are referred to as quiescent states. This last term is used here to cover all cases of suspended activity, etc., from dormancy to sleep. Diapause has been used synonymously with dormancy.

The term dormancy should be restricted insofar as possible to (1) a condition in which no further activity or progress can be induced until certain physiological changes of a physico-chemical character have taken place, such as the taking up of water, the production of certain enzymes, the excretion of urates, etc., and to (2) a definite state of sleep or inanition in which the normal physiological processes

an active animal are substituted by others characteristically dif-
rent; for example, in a mammal, the failure to maintain a constant
mperature and normal respiration. One of the aims of study of
is subject should be to distinguish definite states of dormancy from
ere inactivity. Frequently, dormancy may be distinguished only
ter experimentation. This may often be difficult but, where prac-
able, it will often afford a basis for further analysis of the effects
external conditions upon quiescent animals and on subsequent
lated phenomena.

In land invertebrates, hibernation commonly, though by no means
ways, is accompanied by dormancy covering a part or all of the
bernation period. True dormancy in such animals is usually
rested development, either of the stage in the life history or of the
organs of the adult, accompanied by inanition. In the develop-
g stages, evident changes in form of the whole organism or of its
rts do not take place. In some cases, practically fully formed
ung remain in the egg, hatching only when the dormancy is ended
5). Here inanition is a characteristic feature, though internal
uctural changes are at a standstill.

Some mammals hibernate in a quiescent state in which they be-
ne poikilothermic, or cold-blooded, and resume normal tempera-
e upon awakening. Others appear to become merely inactive
en the weather becomes very cold. Such animals come forth
food when it becomes warm. Hibernation and aestivation in
rs, some squirrels, some reptiles, and many insects (Weese 960),
pears to be merely temporary inanition which may be induced by
d, dryness, lack of food, or lack of oxygen. (659a.)

Since enzymes appear to play an important rôle in initiating the
ive and inactive periods of animals subject to inanition, they are
ated here and from this viewpoint. They have long been credited
h bringing about changes in activity in animals with complicated
cycles, especially insects.

II. PHYSIOLOGICAL LIFE HISTORIES (812)

The term physiological life history is applied to the sequence of
siological states through which an organism passes from the
ually mature adult to the same state in the next generation. It
also been defined as the life history of an organism as controlled
its physiological reactions, either spontaneous, or responses to

the environment. The sexually mature adult is the necessary starting point, because the adult usually places the young under conditions suitable for their development, either as eggs or later stages. These are sometimes carried by the adult and to some degree influenced by the surrounding conditions. In the case of animals which live but one year and have but one generation per year, the relation to the annual cycle of seasons is simple. There are, however, three or four other kinds so that a convenient list of types of physiological life histories may be made out and the various species of any locality for average years will fall into categories. Many of the same species will vary geographically so as to fall under several categories when the population of the species is taken in its entirity. The life history types are enumerated below, followed by a statement of the types of modifications and variations which occur with variations in climate and weather.

1. Those in which the annual cycle and life history cycle agree and the life history occupies but one year. This group is not necessarily distinct from the second, fourth, and fifth, as in some cases the same species may have two generations in one locality, and take two years for development in another, or in a few cases may breed practically continuously under the uniform conditions of the laboratory. Dormancy may or may not occur.

2. Those in which the development of the animal occupies two or more years, so that adults are produced every two or more years. Usually the population is so distributed as to have some adults appear every year but occasionally as in cicadas there are long gaps between appearances. These also vary with climatic conditions as indicated under number 1.

3. Those in which the adult lives over a number of years and reproduces a number of times. It appears that the adults, especially the females, go into a physiological state as regards reactions which is similar to that of the young. This causes them to select a place suitable for the young. They also may return to the same place to nest (birds) and the young may also return to the vicinity of the birth place (birds and salmon).

4. Those in which there are a number of generations in each year. This group is subdivided naturally into those which require a rest period (dormancy) and those which do not. There is in many cases no distinct difference between these and those types described under number 5.

5. Those which reproduce continuously either because of uniform nditions or at different rates under varying conditions as is the case some plankton organisms, and probably many animals in deep ater benthos, tropical rain forest, and other places where there is tle annual rhythm.

Dormancy occurs in representatives of all the groups except posoly birds but in the mammals it is usually represented by standill in embryonic or foetal life and (or) in dormancy during bernation (659a).

III. EXAMPLES OF QUIESCENT STATES

1. *Aquatic animals*

There are many dormant stages in aquatic animals (339). Euanchipus eggs must be dried and in the case of some species frozen fore hatching. Sponge gemmules and the statoblasts of polyzoa, a rule, appear to be benefited by freezing. Some of the dorancies of temporary pond animals may be prolonged over several ars. There has been but little physiological analysis of such enomena in aquatic animals. The different rôles of physiological anges, of enzymes, of mere rotting or mechanical rupture of covergs have not been distinguished.

2. *Land vertebrates* (147, 593, 664, 710–712, 756)

The hibernation and estivation of land vertebrates have been studied nsiderably from a physiological viewpoint. There has also been nsiderable speculation as to the origin of dormancy. Cleghorn 70) has summarized the physiological modifications in mammals as spension of heat regulation and modification of digestion and resration. Carlier (147) has discussed the subject in general terms mammals in particular. Simpson (846) finding that wooducks did not hibernate if they were fed all winter, concluded that k of food was a factor. Since hibernation is induced by CO_2 der experimental conditions, it would be wise in conducting exriments on mammals to analyze the air in the burrows as well as provide or withdraw food. In Simpson's experiments (845, 846) e air was probably changed more often than in the normal burrows 32, 569).

A little work has been done on reptiles and amphibians. Some

of Townsend's (903) work on the toad indicates that the skin of an hibernating animal may allow the passage of water through to the internal tissues, more slowly than does the skin of a non-hibernating animal (255, 256, 588, 721, 722). Absorption of water may also be a factor in the breaking up of dormancy. Observations indicate that the first warm soaking rain in the spring brings out these animals in numbers and marks the beginning of the annual migration to the ponds. Toads dug out of the ground in spring are usually plump and moist. A similar condition has been observed in arthropods which have taken up much water.

3. *Land arthropods* (406, 492, 645, 770, 771, 859)

The most important hibernation and estivation phenomena in general physiological and practical work are those of land arthropods, especially insect pests. The general conditions of the usual winter and spring progress may be illustrated best by the behavior of various invertebrates which are dormant in winter. There are two distinct conditions in the overwintering period:

(1) The dormant condition, characterized by failure to transform into the next stage, e.g., the pupa, no matter how long the exposure to favorable conditions for transformation.

(2) The developmental or preparatory condition, characterized by developmental processes leading to the next transformation (pupation, oviposition, etc.).

The length of the true dormant period and the preparatory period appears to vary considerably either with the generation and the conditions or without apparent reason. For example, if the larva of the alfalfa chalcis completes its development in a dry seed, it goes into a resting period which may last for months. Pupae of some insects appear to behave similarly.

Overwintering adult tiger beetles resume activity and pass a *pre-oviposition* period. One of these (*C. hirticollis* Say) becomes dormant in August and continues so all winter. There is no apparent factor in the summer environment to cause this quiescence. Individuals of other associated species do not do so until later.

In general, the period between the beginning of aestivation or hibernation and the beginning of the next stage in the life cycle is then divisible into two parts: (A) the *dormant period* and (B) the developmental or preparatory period which occurs normally though

;en in abbreviated form in non-dormant generations where it is
nmonly known as the *pre-oviposition* period, (tiger beetle, (812);
lling moth, (826)); the *pre-pupal period* (tiger beetle, (803); cod-
g moth, (826)), etc.

ı. Specific examples. Breitenbecker (113) has shown that desic-
;ion causes the beetles of the genus *Leptinotarsa* to pass into a
.te of "induced" dormancy. Beetles, dormant in dry soil, some-
ıes migrate through the soil to a more moist locality. Long rains
l hibernating beetles. Too dry soil also kills them. Light rains
en cause emergence from dormancy. Emergence was produced,
Breitenbecker's experiments, by moistening the soil, and the
etles reacted negative to gravity and positive to light. Beetles
noved by sifting the dry soil gave no response to light or gravity.
hen placed in moist air until they had absorbed an appreciable
ight of water, they reacted the same as did those in the moistened
l. At temperatures above 14 to 16°C. addition of water caused
ergence; below 14 to 16°C. it did not cause emergence. Duration
dormancy depended on temperature in moist conditions and upon
isture in arid conditions.

Tower's (902) observations relative to hibernation of beetles were
follows: The second brood of the year hibernates in northern
alities. The insect first devours a large amount of food, storing
ıp in the fat body as a reserve. It then ceases to feed and "pre-
res" for hibernation by emptying the alimentary tract and elimi-
ting all excessive waste products through the Malpighian tubules
ıree to ten days). Thus 30 per cent of body weight is lost, 3 per
ıt being alimentary waste, 27 per cent watery material. The
etles then burrow into the ground and hibernate (345). If they
ınot burrow they remain active but cease to feed for several weeks.
on emergence, changes take place in reverse order—waste products
voided, weight and water content increase, protoplasm becomes
tery, etc. Specimens kept in a cage where temperature was high
l moisture low, hibernated for a year and a half, emerging when
moisture content of the soil was increased.

3odine (107) made experiments on grasshoppers of several species.
th increasing body weight and age, a progressive diminution in
relative water content took place. A growing animal had the
ximum percentage of water (75 per cent). Increases in water
ıtent, body weight, and solids took place rapidly at 38°C. Loss

of water was rapid in a dry atmosphere. In a moist atmosphere, body weight and water content increased. The percentage of water differs for different species. *Melanoplus femur-rubrum* had the highest water content of those studied. In *Chortophaga viridifasciata*, during hibernation, the water content fell from 72 per cent to a minimum of 65 per cent. With the approach of cold weather, the animal began to gradually lose water down to 65 per cent.

Weese (960) has shown that young spiders emerge from the winter cocoons only if the humidity of the surrounding air is high. Babcock (48) finds that moisture is important in the case of the corn borer and concludes that there is a progressive adjustment, or acclimatization, to new conditions as the animal invades new areas.

b. Hibernation of codling moth larvae. In addition to the adult potato beetles, grasshoppers, and the muscid larvae, the codling moth larvae have received considerable attention (67, 826, 903). Studies of this species show the practical importance of dormancy in insects, inasmuch as the conditions favoring the breaking of dormancy also favor winter survival, short pupal stages, and successful rapid development the following spring.

Near Urbana, Illinois, dormancy has already begun in many codling moth larvae by the time they have arrived under the bands placed about the tree trunks to catch them, beginning about August 1. Field observers have stated that the initiation of dormancy in summer and autumn larvae is due to exposure to a temperature of 11°C. or thereabout. Two hundred and five larvae were collected in the summer of 1920 (826) between July 22 and August 14 and subjected to temperatures varying from 4°C. to 10.5°C. These larvae were divided into four classes: (a) pupating, (b) failing to pupate because of dormancy, (c) escaping from the corrugated pasteboards, and (d) dying. Those dying and escaping were ignored; only those remaining alive in the pasteboards were considered as having been experimented upon. After those dying and those escaping were deducted, there remained 118 larvae, a part of which were grouped as follows:

July 22 to 28............ ...18 larvae, 17 per cent failure to pupate (dormant)
July 31 to August 3.........37 larvae, 38 per cent failure to pupate (dormant)
August 7 to 8...............28 larvae, 89 per cent failure to pupate (dormant)

)uring the period July 22 to August 8 there had been no mini-ıum outdoor temperatures below 14°C.; all larvae collected in hat period, therefore, were experimentally subjected to temperatures elow 10°C., in order to make them comparable with larvae collected n August 9 and August 10, when outdoor temperature in the early ıorning fell to 11°C. The lots collected August 9 to August 14 17°C.) showed 88 per cent failure to pupate. These experiments howed no indication of cool night effects but rather indicated a sea-)nal increase in the number of individuals failing to pupate, begin-ing about August 1, regardless of minimum temperatures.

The effect of summer and autumn rainfall on the length of time) pupation of hibernating larvae is suggested by the following ata:

Case a: One hundred and eight larvae collected August 20 to eptember 12, 1919. The average time to pupation under favorable onditions in January was 19.3 days at 28°C. and 21.5 days at 17.5°C.

Case b: Larvae collected October 20 of the same year (1919) and reated exactly the same as those in Case a. The time to pupation 50 per cent of them pupated) was 17.8 days at 28°C. The differ-nces between those collected on or before September 12 and those ollected on October 20 were thus very striking. The differences e in the weather conditions between September 12 and October 20, 919. There was very little rain during the period of collection in ugust and the first twelve days of September, but the first twenty ays of October were very rainy and great variations in temperature ccurred.

The foregoing discussion of the codling moth is introduced be-ause the phenomena under consideration are important to the ıccess of the species and, accordingly, have practical value in apple rowing. When the autumn months, September, October, and ovember, respectively (fig. 62) have approximately 88, 125, and 100 ım. of rain or more, or in some cases when the months of De-ember and January are rainy, 95 per cent of the overwintering larvae ırvive, regardless of the usual low temperatures, and the following eason is likely to be one of extreme abundance. This was true in outhern Illinois in 1926, following an autumn and winter of rela-vely heavy rainfall.

IV. THEORIES AND POSSIBLE CAUSES OF DORMANCY

There has been much speculation on the causes of the initiation of dormancy and of its termination. The beginning of a cold or dry season has usually been supposed to cause the initiation of dormancy, and the approach of a wet or warm season is usually cited as the cause of its breaking up. That freezing is necessary to the breaking of dormancy, is also a common assumption. Except for the cases in which there is no dormancy but merely cessation of activity with cold or dryness, the first two explanations have not found much justification, though induced dormancy has been noted in some experiments. These afford some evidence of the underlying causes of the initiation of dormancy.

1. *Initiation of dormancy*

a. Roubaud's theory[1] (748). The only really comprehensive hypothesis of the nature of dormancy so far advanced, is that suggested by E. Roubaud, and has to do primarily with its initiation. His hypothesis is based largely on experimental work with the anthomyid, *Mydaea platyptera* and certain other higher Diptera, and, while apparently applicable to these insects and some others, is probably not of as wide significance as its exponent appears to believe.

Briefly stated, Roubaud's theory is that dormancy in the various

[1] The writer is indebted to Mr. N. J. Atkinson, formerly of the Entomological Branch of Canada, for preparing the seven paragraphs on Roubaud's theory and for general assistance with this chapter.

FIG. 62. Rainfall and codling moth abundance (826).

A, *B*. Limits within which the mean monthly rainfall and temperature fell when plotted for years when the codling moth was scarce and abundant, respectively, in southern Illinois. The areas enclosed by graphs numbered 1 to 12 include the data for the months January to December over a period of ten years (1914–1924). The centers of these areas are represented by crosses numbered similarly in figure 62, *A′* and *B′*.

A,′ *B′*. Ball-Taylor diagrams of temperature and rainfall. *A′* is for a typical year when codling moths are abundant in Southern Illinois; *B′* is for a typical year when they are scarce. The numbers 1 to 12 on each diagram indicate the months January to December, and the cross beside each number indicates the amount of rainfall and mean temperature for the month. (5_1 = first half of May. 5_2 = second half of May.) Note that in the abundant year the rainfall is comparatively heavy (100 to 125 mm.) in September, October and November and comparatively light (25 to 75 mm.) in the spring and summer; while in the scarce year it is light (25 to 50 mm.) in autumn and winter and heavy (100 to 150 mm.) in spring and summer. Note also the higher temperatures in May (5_2), June (6), and July (7) in the abundant year.

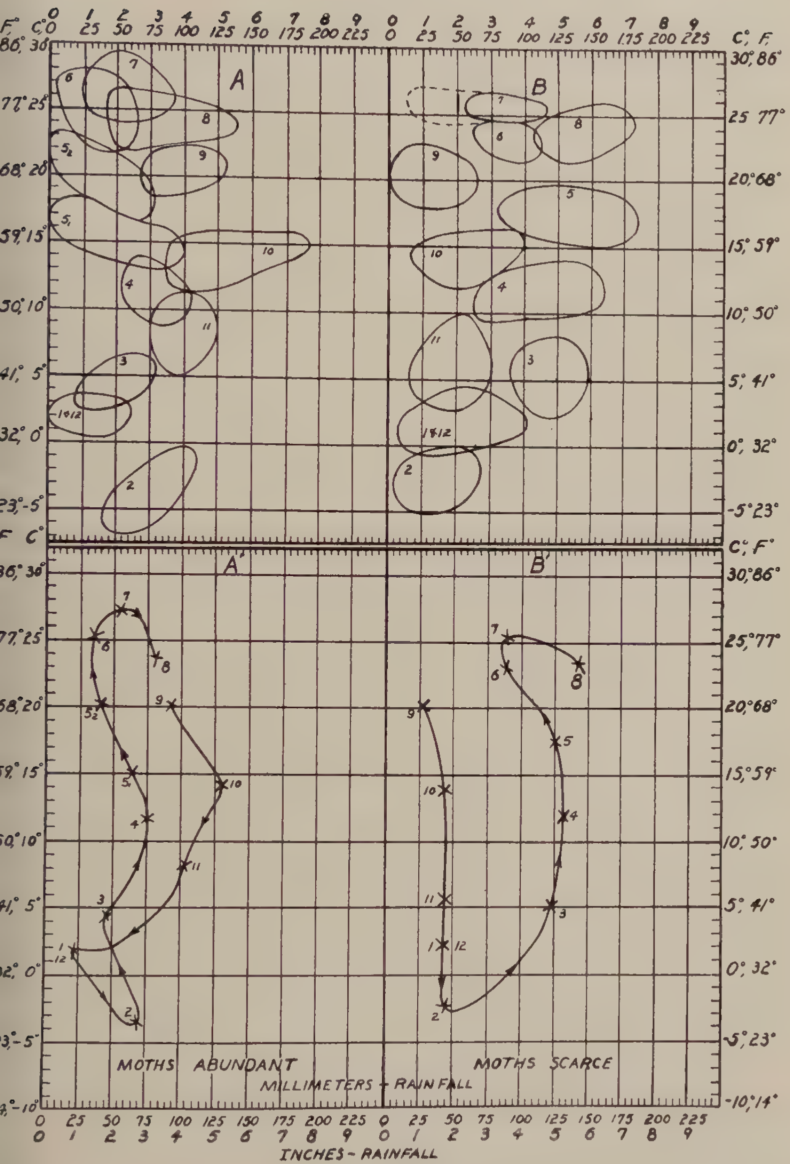

A
B
A'
B'
MOTHS ABUNDANT
MOTHS SCARCE
MILLIMETERS - RAINFALL
INCHES - RAINFALL
C°, F°
30°, 86°
25°, 77°
20°, 68°
15°, 59°
10°, 50°
5°, 41°
0°, 32°
-5°, 23°
-10°, 14°

FIG. 62

insects worked with is due to an auto-intoxication by the excessive secretion of urates, the excretory system during a period of rapid metabolism being unable to dispose of all the waste products formed.

This period of *asthenobiose*, as he terms it, must then, in nature, be succeeded by a period of low temperature, *athermobiose*, or sometimes desiccation, *anhydrobiose*, during which time the general metabolic activities of the insect are greatly retarded while the process of excretion continues with less retardation.

Roubaud separates the higher Diptera into two categories, homodynamous and heterodynamous. The first comprises those forms in which reproduction can continue indefinitely, generation after generation, without any resting period or period of purification being necessary. *M. domestica* is cited as an example. In the second class, he includes those forms in which successive generations of the same annual cycle exhibit dissimilar biological activity and gives as examples *M. platyptera* and various sarcophagids.

A second separation is made into those forms which show a rhythmic asthenia, that is, in which the period of spontaneous inactivity occurs in every generation, and into those showing a cyclic asthenia, a condition apparently identical with that which the writer had previously termed heterodynamous.

Roubaud's conclusions are based largely on a series of experiments which another writer has characterized as "ingenious but not very exhaustive," and on histological examinations of the tissues of the organisms studied. From his experiments he concludes that *M. domestica* and *Stomoxys calcitrans* L. exhibit no rhythm of winter inactivity, the larval hibernation being induced purely by cold. In *Lucilia sericata* he finds a rhythm of winter inactivity independent of cold which may, however, be broken by submitting the dormant larvae to various stimuli, such as extreme variations in humidity or temperature or prolonged submission to cold. *Sarcophaga falculata* and *Mydaea platyptera* are cited, respectively, as examples of pupal and larval periods of winter inactivity independent of cold but yielding only to prolonged submission to low temperatures.

In histological examinations of *M. platyptera*, Roubaud found that the cells of the fat bodies of larvae of the first generation when ready to pupate and those of the second generation on entering the dormant period appeared equally charged with urates. After a prolonged period of submission of larvae of the second generation to cold (5°C.), he found that these urates had almost completely disappeared.

Apparently, the first process to take place upon submission of the ormant larvae to low temperatures is the emptying of the Mal-ighian tubules. During the subsequent prolonged period of dor-nancy there is a gradual transfer of the urates from the adipose tissue o the Malpighian tubules, which show a very marked hypertrophy t the end of the dormant period.

According to Schindler (*fide* Packard) insects of different stages ollected in winter differ very much in their urinary secretions. The ubes of the adults were empty and those of the larvae were full. In otato beetles Fink (292) failed to confirm Roubaud's contentions and oubts their general application.

b. Suggested causes. Dryness causes the initiation of dormancy n potato beetles (Breitenbecker, (113)). According to Payne 654) cold causes an increase in osmotic pressure in the insect body uids which is probably due to loss of water. Tower (902) states hat potato beetles lose a quantity of excreta and considerable water efore entering hibernation. Townsend (903) states that codling noth larvae and toads lose water about the time of the beginning of ibernation. Spooner (857) found that plump codling moth larvae which looked like those which pupated contained much catalase s compared with individuals having the appearance of larvae that id not pupate. Dormancy has been induced in mammals by urying them in the ground or by increasing the CO_2 in the surround-ng air. None of these observations are inconsistent with Roubaud's heory; the cause of the loss of water may be intoxication with excre-ory products as well as cold, and enzymes may be correlated with oth processes.

Parker and Thompson (645) find that the gonads in the larvae of he two-generation corn borer (which passes the winter in the larval tage) are larger than in the one-generation borer, so that in areas where the one- and two-generation types are mixed, it is possible to eparate them by the size of the gonads. They in fact found an pparently practical index of the number of generations. Spooner's 857) determination of catalase was for the same purpose but hardly arried to completion. Both methods are open to the objection hat the larvae have to be killed, and, accordingly, a large number nust be used to determine the proportion of those likely to pupate nd those destined to hibernate. This line of investigation suggests n influence of hormones in the continuation of development or the

production of dormancy. Cahn (141) has attributed migration to such causes.

Bodine (108) found that catalase did not change in grasshoppers with hibernation although CO_2 output decreased. There is probably no true dormancy in the grasshoppers he studied.

2. Breaking of dormancy

a. Roubaud's theory. In so far as this theory is concerned with the transfer of urates from the fat body to the Malpighian tubules, it is to be regarded as a theory of the breaking up of dormancy because this transfer occurs in the period of *preparation* of the pre-pupal stage for the *beginning* referred to (p. 154) as condition (1); condition (2) is the prepupal, preoviposition, etc., period which occurs in non-dormant generations though in abbreviated form. The codling moth prepupal stage covers 1330 developmental units in summer larvae and approximately 2500 in hibernated larvae but it has not been definitely determined because the starting point is not known. Evidently it may often be less than this.

b. Townsend's water enzyme theory (903). The break-up of dormancy in the codling moth larvae, as has been suggested, is easily brought about by addition of water in the animal's body. Diluting the fluids probably speeds up enzyme action. The same hypothesis may be applied also to other animals. In the case of the spiders (Weese (960)), high atmospheric humidity necessary for emergence from the winter cocoon probably adds water to the tissues and speeds up enzyme action. In the grasshoppers an increase of body fluids takes place before the animal can continue to grow and develop in the spring. In the toad a warm spring rain may increase the dilution of body fluids, thus increasing enzyme action and speeding up metabolic processes. According to Townsend, the experimental data already described, when correlated with the published work of other investigators, justifies the belief that an important factor concerned in the breaking-up of dormancy of cold-blooded animals is the reabsorption of water by the tissues. He calls attention to the fact that various workers, have shown that the beginning of hibernation or dormancy in cold-blooded animals is often marked by a reduction in the water content, and it is equally true that the breaking-up of hibernation is usually marked by a taking-in of water.

This difference in water content is perhaps the most universally

recognized difference between the hibernating and non-hibernating animals among cold-blooded types, and may well serve as the starting-point for a theory of hibernation and dormancy and a working hypothesis for the study of the subject. Enzymes must also have prominent places in the hypotheses of investigators of this subject.

Townsend concluded that there is some essential process in dormant larvae which goes on well only at low temperatures. It appears to go on most rapidly at 10°. It proceeds slowly at 0°C. and slower at temperatures above 10° than at 10°. The process seems to be favored by high water content resumed after a concentration of the body fluids. An enzyme or some condition affecting an enzyme, such as hydrogen-ion concentration, would be likely to show such characteristics. He overlooked Roubaud's paper, but his explanation is equally probable.

The delayed emergence of certain individuals may best be construed as parallel with the longer pre-pupal period of individuals which obviously have not received the proper treatment to completely overcome dormancy. This may be due to a failure to develop a sufficient variety or quantity of enzymes, to a failure to take in sufficient water or to develop the proper hydrogen-ion concentration. Some larvae, no doubt, may be disadvantageously located for securing water, or may not take it in as readily as others. Again, Roubaud's explanation, extended to cover incomplete removal of wastes, seems equally applicable.

It is noteworthy that the larvae that seem best prepared for rapid passing of the pre-pupal stage also pass the pupal stage rapidly. This suggests that the two processes are related and that, when the internal physical and chemical conditions are best for completion of the pre-pupal stage, they are also best for the completion of the pupal stage. Townsend showed that larvae soaked in water gained in weight. He soaked larvae two hours per week during storage at the temperatures given below with results as noted.

(1) Soakings increase percentage of larvae pupating, whether the soakings are applied at low temperatures (10°C.) or at high temperatures (30°C.) or both.

(2) Soakings at 10°C. in storage shorten the length of time to pupation.

(3) Soakings at 30°C. (during development) shorten the length of time from pupation to emergence.

These results justify the hypothesis that some process goes on at 10°C., is affected by soakings, and is intimately concerned with the later stages of metamorphosis.

The effects of the addition of water to dormant codling moth larvae may be explained on a physiological basis, and a consideration of this case points the way toward an understanding of its effects in other animals. The break-up of dormancy (condition A) in the codling moth larva is probably marked by the beginning (condition B) of the structural changes leading to metamorphosis, namely, the beginning autolysis of larval tissues which is followed by growth and development of the pupal organs. This should be made the subject of microscopic study.

Bishop (93) has shown that accumulation of acid in the body of the honey bee larva is the probable cause of autolytic processes there, and that enzymes are not important. The summer brood of codling moth larvae do, however, pupate at higher temperatures and the winter enzyme would not be able to work under those conditions. We may explain autolysis in the summer larvae on the basis of acidity. Bishop (93) found that in the bee larva, acidity of the tissues was increased by activity of spinning, assimilation of fats, and other causes. The case of the bee larva is similar to that of the summer brood of codling moth in that the metamorphosis is rather rapid and goes on at relatively high temperatures. (128)

Autolysis may, however, be due to various factors (92). Recent writers have emphasized not only acids but enzymes (110) as active in the breaking down of larval tissues. It has been found that the formation and destruction of fat in the larva of *Calliphora* are processes governed by an equilibrium condition under the action of enzymes. Various writers mention enzymes as being responsible for autolytic processes in tissues.

V. ENZYMES

Since enzymes usually play a rôle in the phenomenon under consideration, it is important that they be discussed. Enzymes do not initiate processes but accelerate those that tend to go on slowly. The acceleration is, however, enormous. Enzymes are associated with living things. They may operate within the cell where various synthetic processes and hydrolytic processes are carried on (935) or outside the cell where digestion takes place. Waksman and Davison (935) discuss their behavior and characteristics quite fully.

1. *Classes of Enzymes*

According to Waksman and Davison (935), the following enzymes ccur in insects and are probably important: Cytases, raffinase, vertase, catalase, and tyrosinase. Several additional enzymes ccur in lower invertebrates.

2. *Enzymes and life histories*

a. Insects (68, 131, 132, 245, 292, 999). Burge and Burge (132) ve shown an increase of catalase from egg to adult for the Colorado tato beetle. Burge believes that increase in catalase brings about increase in metabolism. Bodine (108) has confirmed these general nclusions on grasshoppers. Zieger (999) has found a definite ythm for catalase in the insect life history, reporting that the talase content is high where rapid growth or metamorphosis is ing on (early larval stages, pupal stages) and low during resting ages. Animals with hemimetabolous development show no differ-ce between the early and late developing organism; but in the lometabolous group (such as Lepidoptera) the youngest larval ages are very active, and the catalase content sinks and reaches its inimum at about the last moult, then rises rapidly, reaches its aximum in the pupa, and falls back again in the imago. It shows us an unmistakable relationship to the development of the sex oducts developing at the expense of the fat body. Hence, ani-als with shorter pupal periods show a rapid decrease in catalase ntent. Bernard found that larvae of *Musca lucilia* contained ycogen, but no enzyme which could hydrolyze it. However, as on as the larvae changed into chrysalids, a diastatic enzyme was rmed and the glycogen was utilized.

b. Toad. The sensitivity of the developing egg of the toad at fferent stages in the early life cycle was studied by Hall (363). ne amount of oxygen released from hydrogen peroxide at various riods of development was determined in two different years by e method outlined by Burge. A comparison of the two years sults shows a striking parallelism; the two curves confirm each other. ne curves indicate a decrease in the power of liberating oxygen from drogen peroxide during a very early period, which is the most nsitive one in the life history.

c. Hen's egg. Winternitz and Rogers (981) have shown a definite crease in catalase for the different stages of the hen's egg, as de-lopment proceeds.

3. Enzymes in organs

Rudolph Zieger (999) discusses catalase in a number of animals. He says:

> Those organs which are chemically active, like the liver and the kidney, show it through a conspicuous content of catalase. This conduct applies as well for the invertebrates as for the vertebrates. . . . . The fat body is very rich in catalase, especially in insects where it plays such an important rôle in metabolism. . . . . It was found that in winter, in the condition of lower vital activity, the catalase content of the intestine of echinoderms, of *Lumbricus*, of snails, particularly, is smaller than in summer.

4. Secretion of enzymes

In animals the *free* (*exo*) *enzymes* are secreted by special organs (glands); some glands, such as the salivary, may secrete only one type of enzyme; others, like the pancreas, may secrete several. The saliva of various predacious insects contains an enzyme which digests the proteins before they are taken into the system (935). Microörganisms secrete enzymes into the culture medium in which they are growing.

5. Regulation of enzymes (935)

Difference in enzyme formation under different conditions is quantitative rather than qualitative in nature. There are comparatively few instances on record in which the formation of an entirely new enzyme is due to the presence of a specific substance or to specific conditions. According to Waksman and Davison, it is not necessary to assume the existence of a specific enzyme for each separate process, for it is possible that the same enzyme catalyzes various reactions, depending upon the composition of the medium in which they occur. Since this medium can vary, several conditions may occur which are suitable for various enzymatic processes.

The same authors make the following statement relative to quantitative regulation:

> The quantitative regulation of enzyme formation in animals is strikingly illustrated by the work of Pavlov on the effect of different nutrients upon the secretion of pepsin by the stomach, and of trypsin, diastase, and lipase by the pancreas. The feeding of milk causes a greater secretion of lipase than a diet of bread or meat which contains the same amount of nitrogen, while a bread meal produces a larger quantity of diastase. The secretion of protease is

imilar after each of these three foods. On the other hand, the enzyme activi-ies of the pancreas and stomach of horses are unchanged whether vegetable or nimal protein is fed. The enzymes of meat eating plants can digest all types of protein equally well. If meat or eggs are fed to seven-day-old infants, the gastric juice acquires the ability to digest these foods, but this adaptation pparently depends upon an increase in gastric acidity; for, if the latter does ot occur, the eggs are not digested.

6. *Proenzymes or zymogens* (935)

Various enzymes are secreted in an inactive form (zymogens) nd are later transformed into active enzymes by an activator. This s true of pepsin, trypsin, and thrombin, which are secreted as pep-inogen, trypsinogen and thrombogen. Other zymogens have also een isolated. Activation in some instances involves the formation f complex organic salts. Activating agents include acids, alkalies nd salts in addition to special kinases. Calcium can activate rypsinogen.

The zymogen of pancreatic juice is activated by bile salts, the ction of which is specific for the pancreatic esterase but does not ffect stomach or intestinal lipase. The optimal concentration of he bile salts is 0.33 per cent in most cases.

A zymogen is regarded not as a preliminary stage of an enzyme ut as a mixture of the latter with a paralyzing substance. Activa-ion consists in the destruction of the paralyzer according to this iew. The transformation of an inactive zymogen into an active nzyme is irreversible. All these phenomena may be of much im-ortance in connection with quiescent states in mammals as well as n lower vertebrates and invertebrates.

7. *Co-enzymes* (935)

Waksman and Davison emphasize the importance of these sub-ances. Co-enzymes, or accelerators, are substances which increase e activity of enzymes. The addition of a minute quantity of man-anese salts causes a great increase in the oxidizing power of laccase. milar phenomena are illustrated by the influence of calcium salts n the activity of pectase, of asparagin on diastase, and of KCl, aCl, $CaCl_2$ and KNO_3 on the diastase of dialyzed pancreatic juice. o-enzymes may be important in connection with quiescent states d life histories.

8. Importance of water, temperature and hydrogen ions

According to Bayliss (68), most enzymes have a hydrolytic action, and their activities are commonly manifested in the presence of an excess of water. He says, "An enzyme action comes to an end or equilibrium point due to the accumulation of the products of the reaction, dilution, or removal of the products." The effect of water upon enzymatic action is well known. According to Fischer:

The point at which the reaction of digestive enzymes comes to a standstill is reached sooner in a concentrated solution than in a more dilute one. In fact, most fermentation mixtures which have stopped will go further if water is added. Each enzyme has an optimum temperature. Each enzyme has an optimum H-ion concentration. Many require a decidedly acid medium; only a few require neutral or alkaline conditions.

9. Relation to autolysis

Whether autolysis in an insect larva is due to acid or to the effect of acid on enzymes, the addition of water might be expected to speed up and increase the action. Thus, Bishop (93) in his discussion of the chemistry of metamorphosis in the honey bee, says:

The differences in rate and extent of autolysis of tissues from different stages, in vitro, are due to differences in acidity of the autolysate. When the tissues are diluted with pure water, the buffering action of the mixture is lowered, and a slight excess of acidity in one tissue or the other would accelerate its rate of autolysis.

This, no doubt, lends importance to the regulation of neutrality in the insect body where tracheal air may prove important. (Krogh 497.)

10. Enzymes and dormancy

The subject of enzymes as a factor in hibernation has been studied by a few workers. The reversible action of lipase is often cited in connection with the stored fat (120) of mammals. Vernon (928) worked on the hedgehog from this point of view. He says,

Hibernation has a considerable influence on ereptic power. The kidney and liver of hibernating hedgehogs contained on an average less than half the erepsin present in the corresponding tissues of non-hibernating animals, while the spleen contained only a seventh as much ferment. Skeletal muscles and brain were uninfluenced by hibernation. The nutrition of hibernating mammals is commonly associated with the reversible action of lipase which stores fat in summer and breaks it down in winter.

Spooner (857) shows that codling moth larvae may be roughly livided into two groups, on the basis of external appearances: those vhich are plump and well rounded may be expected to pupate, vhereas those which are thinner will not. The former class conains the most catalase.

VI. METHODS OF STUDYING QUIESCENT STATES

Quiescent states, which have received comparatively little atten-ion in most general studies, need to be investigated with much more han the usual care and preparation. The conditions of animals in utumn and winter are not infrequently the results of conditions uilt up in the month of July or August. The conditions in spring nay have been determined the preceding spring or summer. The atter case is illustrated by the appearance of *Eubranchipus serratus* iear Urbana, Illinois, thirty days later than usual in 1927 following very wet autumn in 1926. This species also appeared in December bout 1900 and was reduced in numbers for some years after as the oung hatching then did not reproduce.

Continuous observation over a period of years is the best method or securing valuable hints as to the dormant periods, the require-nents for breaking dormancy, and the relation of dormancy con-litions to abundance of individuals and rate of development in ater stages. Several stations should be selected for such observa-ion while experiments are in progress, for the differences between ears may afford valuable information.

1. Collecting material for experimental work

Collections of insects and other arthropods should be made daily r oftener, beginning a month or more before dormancy is expected o set in, and continuing until well past the maximum appearance f the stage showing dormancy. In all cases, it is very important to nake careful observations of the activities of the animal in its native aunts during the beginning of the dormant period and, wherever ossible, to measure its general progress throughout the period. Careful notes must be made on the conditions of weather preceding ollections and the food of the stage, as indicated by the food plant, practicable.

When the collection of vertebrates precedes the beginning of dor-nancy, the greatest care must be taken to see that the normal

food is supplied or to determine whether the food and the changed conditions influence the beginning of the dormant period. Hibernation and aestivation of vertebrates can be studied best where the animals can be observed in their natural haunts. Simpson (846), for example, caught woodchucks with box traps and placed them in artificial burrows opening into a central court. (He does not state whether the court was covered or not.)

There is hardly a subject demanding such diversified training as the study of quiescent states. Histological and cytological studies were carried out by Roubaud and suggested by Townsend. Work on enzymes demands a thorough training in quantitative analysis, physical chemistry, and organic and biological chemistry. The requirements for the study of autointoxication (Roubaud) are not less exacting. All the resources of the experienced naturalist and ecologist must also be brought into play. It is true, however, that some investigators have met with success in work on enzymes without all the training just implied. In working up the subject of enzymes citations 6, 280, 281, 631, 745, 855, 856, 935, 936, and 983 should be consulted.

From the standpoint of economic entomology it appears that the subject of physiological life histories, especially where dormancy is involved, is of much importance as controlling the vigor of overwintering populations, their rate of development, rate of reproduction, and general success. From a theoretical standpoint, especially that of genetics, it affords new problems, such as the "cytoplasmic heredity," and the control of numbers of generations by conditions operating on the grandparents.

CHAPTER VII

Animals in Relation to Temperature

I. INTRODUCTION

In moist temperate regions, temperature is a very important ctor and is naturally the first factor which one attempts to evaluate the maze of interlocking factors operating in a biotic community. he rate of metabolism and rate of development, which are closely rrelated with the success and abundance of animals both warm and ld blooded, are influenced by temperature. In order to study the lations of metabolism to temperature it is necessary, in so far as practicable, to vary the temperature alone, under exact laboratory nditions.

It is the purpose of this chapter to establish a scientific basis for e measurement of development in terms of *thermal units*. In order establish this basis and to make clear its relations to current re- arches and theories, the following principles are regarded as valid r poikilotherms.

(1) Standard metabolism changes in rate as temperature is varied a manner not altogether discordant with Q_{10} as a constant but nforming more closely to Arrhenius' formula.

(2) Activity and development on the other hand do not conform either of these laws but do conform *in part* to the century-old idea the equilateral hyperbola.

(3) The portion of development which so conforms is that which kes place in about one-third the possible range in degrees. This ird begins about one-fifth the range above the minimum.

(4) The lack of conformation to the equilateral hyperbola renders *possible* all direct use of natural temperatures for "summing."

(5) The amount of energy exchange or work to be done in the aturing of an organism or completing a stage in the life history is ually a constant total (for individuals of a given population) ough acclimation phenomena may modify the physical and chemi- l constant without changing the rate.

(6) The effect of one degree for one hour within the range of tem-

perature characterized by the "hyperbolic rate" is the unit (thermal) of measurement of the rate and amount of development.

Methods of calculating the standards from experimental data are discussed in this chapter, together with examples. The survival of animals under adverse temperatures is also discussed.

II. STANDARD METABOLISM

According to Krogh (500), standard metabolism is the metabolism of minimal functional activity which is taken to be obtained when voluntary muscular movements are eliminated and no food is being

TABLE 12

Standard metabolism of different animals per unit of weight and per surface area at 20°C. Conditions are essentially those for basal metabolism. In most of the cases, metabolism has been calculated from O_2 absorption: 1 liter O_2 equals 4.8 Calories (after Krogh (500))

ANIMAL	WEIGHT KG.	CALORIES PER KILOGRAM AND HOUR	CALORIES PER UNIT SURFACE AND HOUR	AUTHOR
Young dog	950.0×10^{-3}	1.16	1.14	Krogh
Frog	30.0×10^{-3}	0.34	0.106	Krogh
Decerebrated snake	34.0×10^{-3}	0.15	0.049	Krogh
Goldfish	9.3×10^{-3}	0.53	1.11	Ege and Krogh (272)
Gnat (Culex)	8.0×10^{-6}	2.70	0.054	Ellinger (273)
Chrysalides of Tenebrio (first)	160.0×10^{-6}	1.35	0.087	Krogh
Eggs of Acilius	1.5×10^{-6}	3.35	0.038	Krogh

digested or absorbed. Muscular movement is excluded with difficulty and many experiments have been seriously impaired by muscular activity. Standard metabolism may be studied under various temperature conditions.

Basal metabolism, in practice, is Krogh's standard metabolism at 20°C. and with animals of standard size, age, diet, and treatment, strictly speaking, after making deduction for the heart and respiratory actions. With the influence of functional activity removed, basal metabolism is about 25 per cent of standard metabolism.

Standard metabolism of animals has been studied by numerous

ıthors. The more important results under the usual conditions of ısal metabolism, as compiled by Krogh (500), are shown in table 12. he greatest probable source of error is the lack of complete suppreson of muscular activity. The results show wide variation in only few of these cases. They are more nearly alike on the basis of ırface area than on the basis of weight. With the exception of the ɔg, the surface values range from 0.038 to 0.112; on the basis of eight the values range from 0.15 to 3.35. Figure 63 shows the curve r standard metabolism of a toad, frog, fish and dog (500) in comıarison with Arrhenius' (40, 41) curves. The lower curve shows the andard metabolism for Tenebrio pupae when CO_2 production is

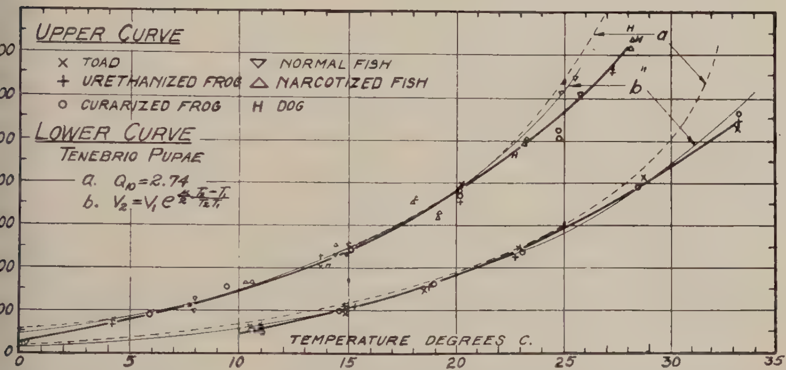


FIG. 63. Standard metabolism in relation to temperature (after Krogh 00)). The vertical scale is cc. O_2 per kilogram per hour. The pupae data e for the period of minimum CO_2 production. Q_{10} and Arrhenius curves are own. (Krogh's Tenebrio scale does not agree with his table.)

west. The curve is essentially the same, but the rate of metabolism lower than in the vertebrates. If the Tenebrio curve were moved the left until the first datum rested on 2°C., it would practically incide with the vertebrate curve.

A curve with Q_{10} constant, 2.74, (Krogh (500)) is also shown but its ırvature is too great; and using other values for the constant does ɔt help very much to give a better fit (853, 854).

The curve of standard metabolism (fig. 63*b*) approximates the law Arrhenius who uses absolute temperatures. From the velocity V_1) of any process at one temperature, the velocity at another temerature (V_2) may be calculated. The formula used in calculating

the curves is $V_2 = V_1 e^{\frac{\mu}{2}\left(\frac{T_2 - T_1}{T_2 T_1}\right)}$ where μ is taken equal to 16,700 (Garrey (327)).

The average for several animals was 141.5 (Krogh's table XVI (500)). The upper curve (b) was calculated by this formula taking $V_1 = 141.5$ and $T_1 = 283° = (t_1 + 273°)$. The lower curve was calculated from 105 as V_1 and 288° ($t_1 = 15°$) as T_1. It conforms closely to the metabolism of the chrysalids of Tenebrio.

It is important to measure CO_2 output and oxygen consumption in connection with experimental work with temperature (see Krogh (496, 500, 501); Müller (609); Bruce (122); Benedict and Homans (74) and others (879, 880)). For this reason it is necessary to consider

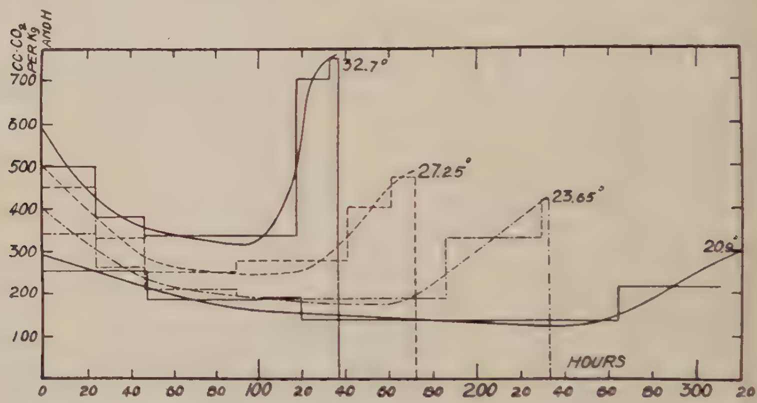


FIG. 64. Showing the variation in rate of CO_2 production during the pupal life of *Tenebrio molitor* at the several constant temperatures indicated (after Krogh, (499)).

the variations which occur during the life of an animal. During the incubation of the hen's egg (Bohr and Hasselbalch (500)), the CO_2 output decreases at first, rises slowly until the tenth day, then rapidly during the next week. After the seventeenth day the CO_2 output decreases. These figures were not reduced to unity of weight. Bohr (109) found that the CO_2 production of the embryo of the snake decreases per unit of weight as the incubation proceeds. The larvae of Drosophila (Fink) show a rapid increase in CO_2 output with a maximum at about mid-larval life.

The CO_2 production of the pupae of a species of Coleoptera (*Tenebrio molitor*) has been studied by Krogh and of two species

f Diptera by other authors (Krogh (500)). In all these cases the O_2 production decreases during the first four-fifths of the pupal eriod and then increases rapidly to emergence (see fig. 64).

It is often desirable to compare the rate of metabolism at different emperatures in connection with climate-simulation experiments. is evident that if oxygen consumption or carbon dioxide output is be used, it is necessary to consider the effects of conditions on andard metabolism.

In the human species the standard metabolism per unit weight is uch greater for young than for adults, and in old age there is a stinct decrease. There are also four periodic daily variations in spiratory exchange, and also seasonal variations. Following uscular training or heavy muscular work over long periods, e standard metabolism increases. Prolonged fasting decreases etabolism.

The curves for activity and for velocity of normal development do ot appear to conform to the curve for standard metabolism, or at ast not over a sufficient range of temperature to make it of practical lue in studies of the relations of organisms carrying on their normal tivity in actual climate and weather.

There has always been discussion and disagreement between those ho would relate the rates of life processes to chemical reaction and ose who would use them for practical purposes, as for prediction future maturity or transformation. To a certain extent at least, e two groups have been working on different problems, using fferent methods. Activity may be considered alone, and the ngths of definite (developmental) stages, in which food-taking and uscular activity are involved, may also be considered.

III. NORMAL LIFE METABOLISM

Standard metabolism has been discussed in the preceding section. rogh took his standard metabolism readings shown in figure 64, hen the CO_2 production was at a minimum. The curves for andard metabolism are concave but rise as the temperature is ised. The metabolism of animals during their life-history stages not ordinarily standard metabolism; muscular activity and the sorption and digestion of food are involved. The taking and gestion of food and some muscular activity are almost continuous ring the growth of those stages which feed. Rapid morphological

changes, not characteristic of ordinary development, take place in quiescent stages, such as egg and pupal stages. In the latter there is an almost complete tearing down of structure.

1. *Relation of activity to temperature*

Verworn (929) long ago drew a curve, figure 65, showing the amount of activity or irritability at different temperatures (517). It was

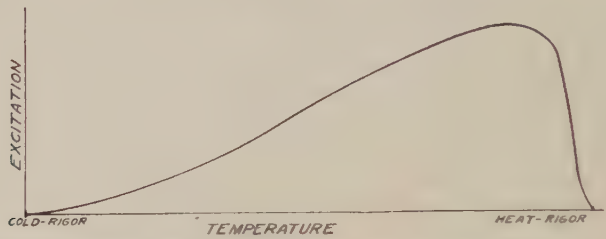


FIG. 65. Verworn's (*Gen. Physiol.*) excitation curve for temperature

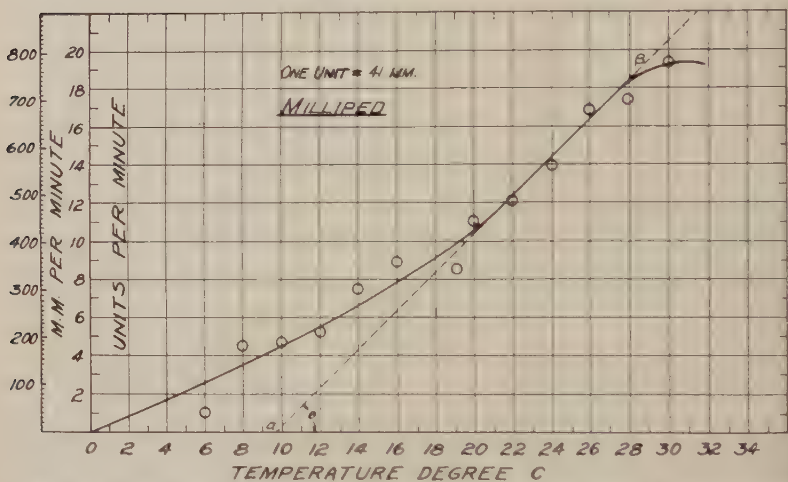


FIG. 66. The rate of progression of a milliped at different temperatures (adapted from Crozier (223)); a thermal unit curve.

based upon general phenomena of excitation but it conforms very well to the curves of more recent origin. Pantin (642) secured most beautiful curves for rate of progression of marine amoebae conforming in detail to the rate of growth of the Indian corn plant. Figure

; (data from Crozier) shows the rate of creeping of a milliped. The timated point at which movement would cease is 0°C. The raight-line portion of the curve lies between 21° and 27°C. Within ese limits, the time to go a definite distance multiplied by the

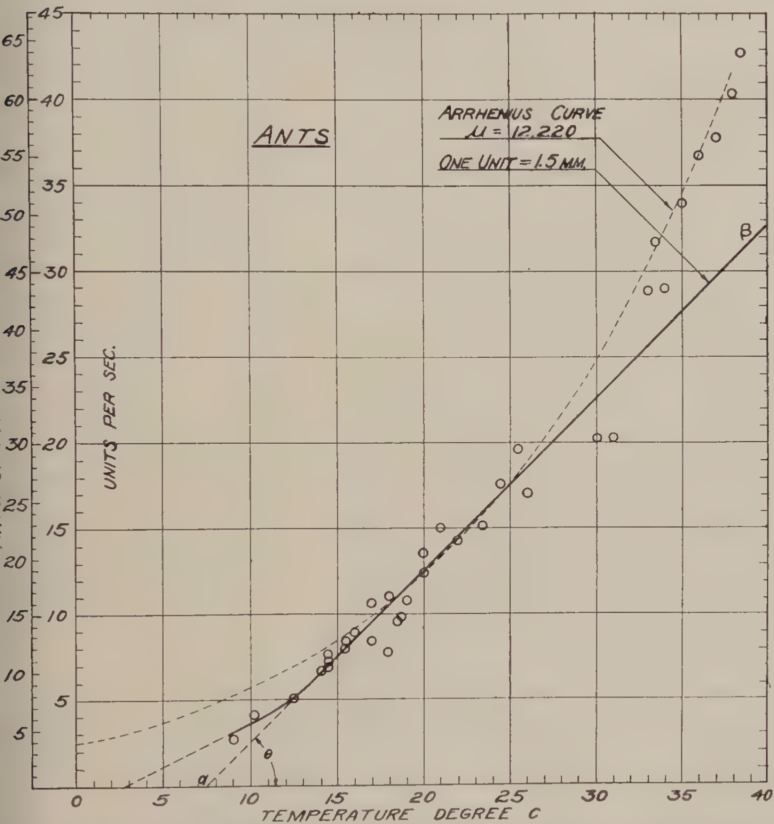


FIG. 67. The rate of progression of a species of ant at different temperatures ter Shapley (800)) with the thermal unit and Arrhenius curve both shown. e data are of interest as the progression at temperatures around 35°C. viates from the usual thermal unit type.

nperature above α is a constant, namely, 144 degree-minutes. ie conformation to the curve of Arrhenius is not good, especially the upper end where it suggests turning down (737).

The rate of progression of ants (fig. 67) as studied by Shapley (800) pears to conform fairly well to the Arrhenius formula above 16°C.

when μ has a value of 16,700. But there is a distinct straight-line tendency between 12° and 30°C., while the higher temperature velocities fall into a second straight line. There is a turning upward at about 30°, which seems quite exceptional but may be due to differences between substratum temperature and air temperature.

Krafka (494) has found that the facet number in the eyes of *Drosophila* varies with temperature. The curves are in part like that for

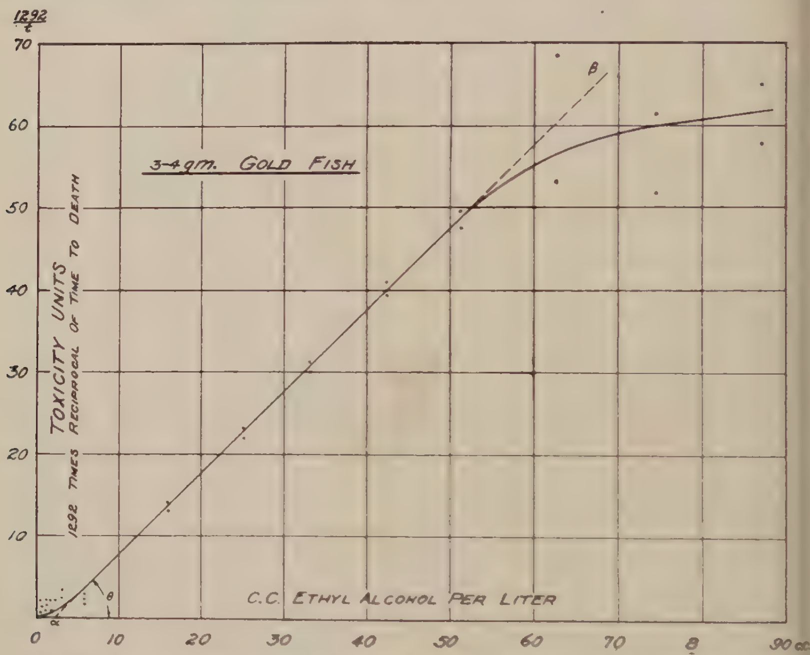


FIG. 68. Time concentration curve for the time to death of goldfish in ethyl alcohol (after Powers (685)). The curve conforms to the temperature type.

the rate of progression of ants and in part like the other curves. The rate of dying of goldfishes is similar (fig. 68).

The rate of chirping of crickets has been repeatedly studied (Shull (842)), and the curves fall into a straight line, between 17° and 26°C. (fig. 69). None of these activities, however, has been studied in critical experiments. The range of temperatures has not been extended to cover all temperatures occurring within the growing season in temperate latitudes. The curves indicate, however, that in a range of temperatures between about 15° and 30° the velocities

ually fall in a straight line. The activities of several insects have
een observed and estimated. The rate of reproduction of the grain

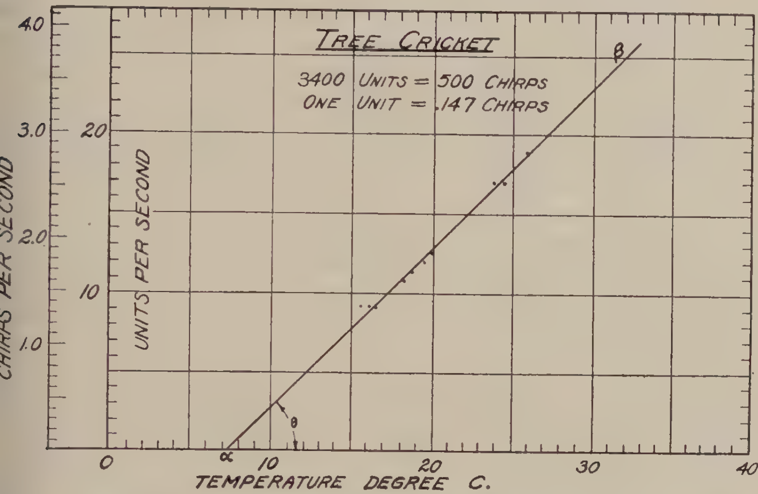


FIG. 69. The thermal unit curve for the chirping of a tree cricket (data from
ull (842)).

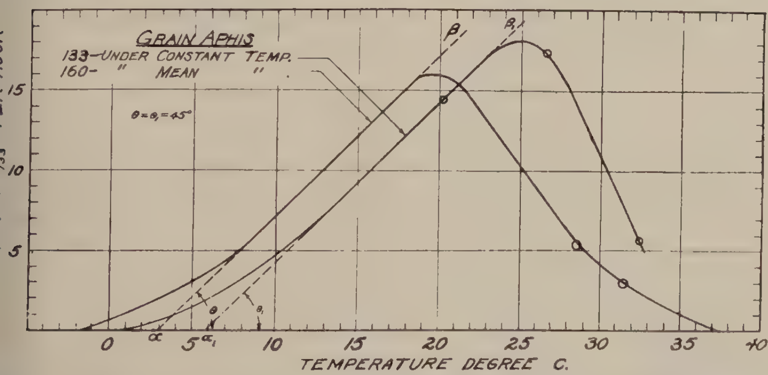


FIG. 70. Thermal unit curve for the reproduction of the grain aphis
odified from Sanderson; data by Hunter (and Glenn (417)) under weather
ditions, and for mean temperatures.
Thermal unit curve for the reproduction of the grain aphis under experimental
ditions (data by Headlee (380)).

his was observed by Hunter and Glenn (417), and the data were
t in the form of a curve by Sanderson (772), (fig. 70). Heart

rates also commonly follow the same principle (Laurens, 511a). In all these cases the velocity is number of beats, number of young born, number chirps or distance travelled per unit of time; and the number of actions added per degree rise for each unit of time is important.

Our chief conclusion is that, for rates of activity within medial temperatures only (about 15° to 30°C.), the time-temperature curve for definite amounts of work conforms nearly enough to the equilateral hyperbola to make it useful in temperature work, and the rates fall nearly enough to a straight line to make the straight-line portion of great value in climatology. These facts do not accord with the Q_{10} as a constant or with Arrhenius' formula (40, 41, 223, 224, 225, 226, 500).

Crozier and others (223–226) have been advocates of the idea that metabolic rates, growth rates, rates of locomotion, etc., conform to Arrhenius' formula and that each dominating reaction has a different constant. Thus whenever the data do not fit the curve assumed, the constant is changed. The so-called critical temperatures are the temperatures at which the changes have been made. These critical temperatures are 4.5°, 9°, 20°, 25°, 27°, and 30°. Brown (121, fig. 2) working on the length of the instars of cladocerans has cut the well-established straight line twice with two changes in the constant value for the curves which he uses.[1]

2. Normal development

In all the cases of activity cited above, the number of actions per unit of time and per degree rise afford the velocity data required. In the case of development, it is necessary to take the reciprocal of time required to complete a stage. The meaning of velocity as applied in this way is well illustrated by reference to rate of movement, or speed of travel, of a machine or animal or man. In all matters of speed of travel, the *reciprocal* of the *time* required to cover a fixed distance is used to represent *relative velocity*, or rate of travel. For example, in the case of a tractor pulling a load 12 miles at various speeds, the relative velocity is obtained from the time as shown in

[1] It is difficult for the writer to see how this is proving anything either relative to the facts of velocity which is represented by reciprocals of time or the chemical processes which within the straight line limits appear to be increasing in rate in direct proportion to the increase in temperature.

ble 13. The reciprocal multiplied by the total miles gives velocity miles per hour. The reciprocals of the time to complete any unit work are thus a convenient expression of relative velocity.

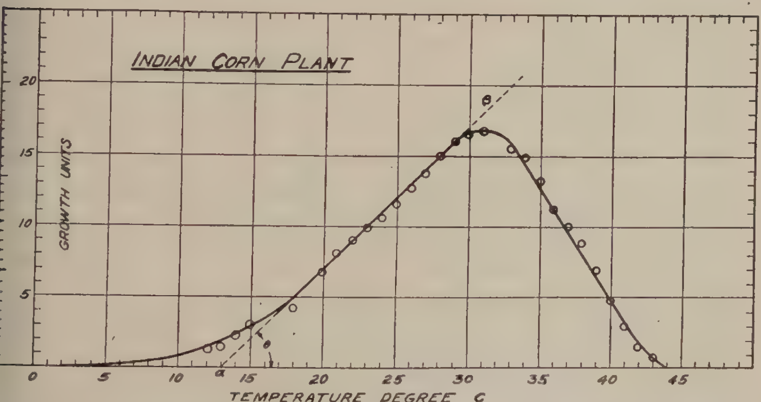
When the normal development and normal activities are conered for the natural periods or stages of animals, the law of Arrhen-

TABLE 13

Example of a tractor pulling a load 12 miles at various speeds

	TIME TO GO 12 MILES							
	2 hours	3 hours	4 hours	5 hours	6 hours	8 hours	10 hours	12 hours
iprocals of time	0.50	0.33$\frac{1}{3}$	0.25	0.20	0.16$\frac{2}{3}$	0.12$\frac{1}{2}$	0.10	0.08$\frac{1}{3}$
es per hour (12 × reciprocals)	6.0	4.0	3.0	2.4	2.0	1.5	1.2	1.0

probably does not apply, much less Q_{10} (445). The natural stages l periods of animals which have been investigated include the owing (Krogh (498)): (1) the formation of the first cleavage plane he frog's egg (*Rana butyrhina*); (2) five different stages of embry-



:G. 71. The thermal unit curve for the growth of the Indian corn plant ng 12 hr. exposures to constant temperatures (data by Lehenbauer (515)).

development of *Rana butyrhina;* (3) first and second segmentation ggs of *Strongylocentrotus* and *Arbacia;* (4) fertilization to hatching ggs of four species of marine fish; (5) eggs of Acilius, fifty-two rs after fertilization, to hatching; (6) the pupal life of *Tenebrio*

molitor (meal worm) (499), of *Carpocapsa pomonella* (codling moth), (Shelford (826)) and a number of other insects (see Sanderson and Peairs (774)); (7) eggs of the codling moth from laying to hatching (Sanderson and Peairs, (774)); (8) the length of life of the grain aphis (Headlee (380)), and many other stages of a similar nature. Hertwig (392, 393) worked on the frog.

When the reciprocal of the time to complete a definite stage is taken to indicate relative velocity at different temperatures, the curves conform to the following form: Slant upward from the temperature at which development begins; concave upward, through

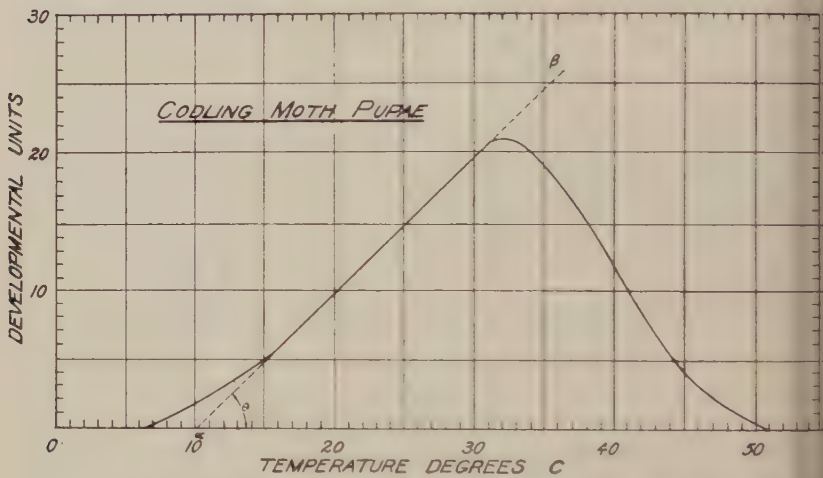


FIG. 72. Thermal unit curve for the completion of the pupal stage of the codling moth. Adjusted to actual weather conditions.

about 10°C.; slant upward, in a straight line, through about 10°C.; then, after gradually changing direction downward for about 5°, the curve continues downward more rapidly than it rose. The form of this curve for normal life processes is confirmed by the growth of the Indian corn plant, by Lehenbauer (515), figure 71, and variable and constant temperature experiments on the codling moth pupa by Shelford (826), figure 72. The Indian corn curve is based upon the amount of growth during twelve-hour exposures. Janisch (432) has recently worked over much data and called attention to the fact that the time-temperature curves are asymmetrical catenary curves

which the velocity and other rate curves treated here are the iprocals. He gives a mathematical treatment and formula. ere are numerous other studies of relations to temperature. wers (685, see also 373) has studied the time to death of goldfish lifferent concentrations of salt, and the curves conform to a straight e for a series of concentrations at the same temperature. For ex- ple, for lithium chloride the concentration was from 0.16 to 0.38 rmal, for sodium chloride, 0.3 to 0.5 normal, and for ethyl alcohol, to 55.0 cc. per liter (fig. 68). These curves turn to the right at higher concentration but none turn downward and none to the ;, as is the case with the rate of progression of the ants.

The idea, now centuries old, to the effect that temperature can summed so as to give approximately the time of development of a ticular organism, must be abandoned wherever accurate results desired. This method is likely to fail more or less completely in unusual seasons when accuracy is most needed (577, 578, 844).

To illustrate the falsity of the assumption upon which temperature- nming rests, the work of Krogh (499) on the pupae of *Tenebrio litor* may be cited. Figure 73, *A*, shows the actual velocity curve the development of these pupae. The solid line is drawn through data of Krogh and extended to conform to other known curves. ure 73, *B*, shows the velocity curve which would be assumed in nming temperatures for the meal worm pupa. The temperature- nming curve is the reciprocal of the assumed time-temperature ve which is an actual equilateral hyperbola. The Greek letter ha is used for the zero of the hyperbola and for the corresponding nt on the velocity curve; this point has only mathematical signifi- ce and is without biological meaning. When correctly drawn velocity curve always makes an angle of 45 degrees and thus ocity values within the straight-line limits are always equal to perature values. It was, in fact, velocity values that were nmed instead of temperature, for it is only in so far as velocity ies are the exact equivalent of temperature values that accurate ılts may be secured.

ll known curves[2] are similar to figure 73, *A*, and none like figure

Mathematicians ordinarily state that the so-called straight line portion ich curves only approximates a straight line. They appear to regard curves as sigmoid. One lot in Krogh's data suggests this, while another cates the reverse. Friend, who wrote on the Birch Leaf Skeletonizer

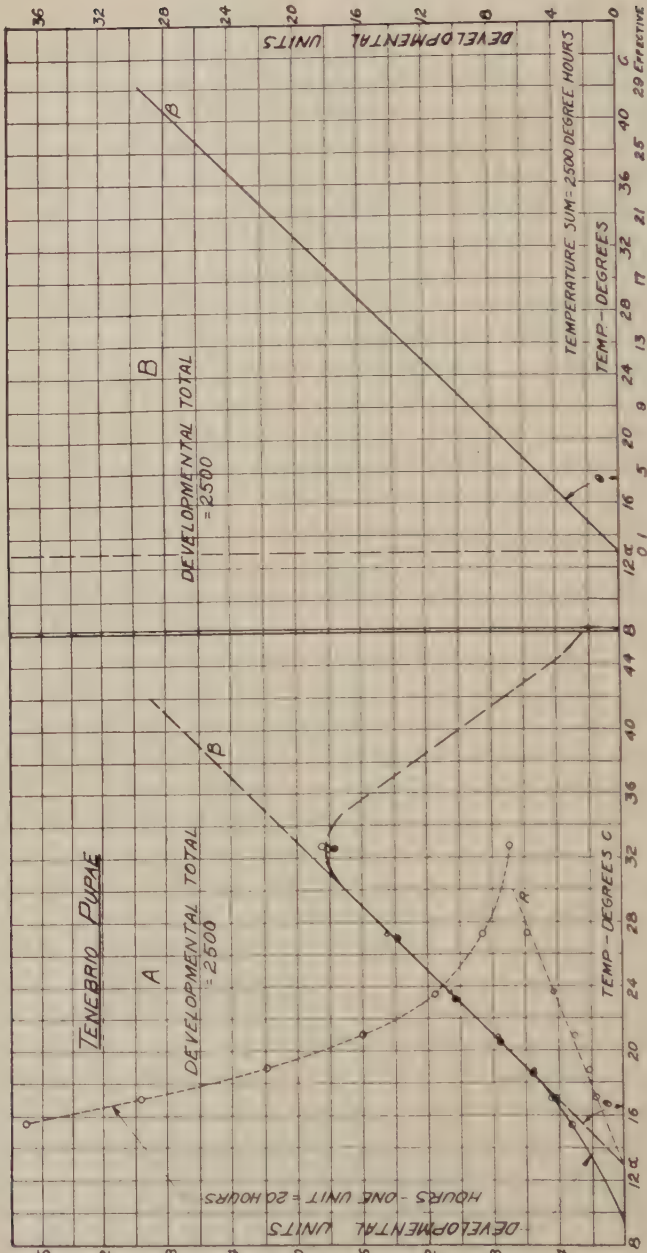


FIG. 73. Thermal unit curve *A* with reciprocal curve *R* and temperature sum curve *B*, based on *Tenebrio molitor* (data after Krogh (499)) and showing the relation between the actual velocity curve (*A*, solid line and points) and the curve assumed in summing temperatures (*B*, straight from 13° to 42°C.).

, *B*. Developmental units may be summed with correct results hen the curve is of the *A* type, but the results are not correct for velopment when temperature is summed. As evidence for the rrectness of the form of curve, not only are the curves of activity ted but also figures 70 and 71. The rate of development of the dling moth pupa as is shown in figure 72, is based upon data from nstant temperature experiments between 11° and 35°, and variable mperature experiments between 10° and 50°, and in normal weather nditions 0° and 40°, but the data were later corrected to conform actual weather conditions throughout. The form of the curve ove 35° is based on trial with various forms of curves by methods scribed on page 195 but with short exposures at the high temperares. It will be noted that both the Indian corn curve (fig. 71) d codling moth curve come to zero velocity at about 45°.

Turning attention to points marked α on these curves, it will be ted that in no case are they correct starting points of development. was pointed out by Johansen and Krogh (445), none of the several ethods of determining the threshold are correct; it is alpha that is tained (824, 826). For nearly two centuries temperatures have en summed on the assumption that α is the starting point for velopment (338).

The "constant" or total work to complete a process (499, 876, 877)

The idea of a constant, so long held by phenologists and used as basis for the summing of temperatures, finds support according to orthrup (627) in Rubner's idea that the total energy transformed r kilo of body weight during the total life of the animal is approxitely constant for a large number of animals. Pearl has also ilized the idea (532, 533).

Krogh's study (499) of the pupal stage of *Tenebrio molitor* is pecially significant because it was done with unusual care and

3a), states that the velocity curve is sigmoid. However, he has a very ited series of temperatures (20°, 21°, 22°C.) which lie very near the center he straight line portion of the curve. To test this assumption experiments uld be run at 15°, 18°, 21° and 24°C., with uniform stock. A greater number experiments covering more temperatures would be desired. In case a ticular curve does prove to be sigmoid, the substitution process (page 284 apter XI) will have to be used practically throughout the curve, in which e the assumption of a straight line becomes essentially a mere method.

especially because the CO_2 was determined during pupal incubation. Figure 73 shows the time-temperature curve (short dash line) for one set of these pupae which conforms to an equilateral hyperbola from 15° to 30°, but with distinct deviations at approximately 13.5° and 14.5°, and again at 32.5°C. The product of time and temperature above α is regular and approximately 2500 between 15° and 30°. The higher and lower values are discordant when a value of 13° is assumed for alpha (see page 188) and deducted from the actual temperatures. The velocity data, plotted as 2500 times the reciprocal of time, fall into a straight line in a manner tending to throw discredit on the application of Q_{10} as a constant, or Arrhenius' formula, though the metabolic rate (fig. 63) at the minimum period for CO_2 production (fig. 64) responds to various temperatures in reasonable accord to the latter. The concavity in Krogh's final series, shown by the rings, is very slight and is not confirmed by the other series. The straight-line relation implies a constant amount of work to be completed.

Evidence of a constant amount of work is shown by Krogh (499). The total CO_2 produced by *Tenebrio molitor* during pupal life is shown in table 14.

Krogh states further that he has made similar observations on the eggs of the water beetle (Acilius) showing that a fixed amount of CO_2 is produced by the eggs during incubation. Tangl implies a similar relation in his several papers (876, 877).

A most important concept must be stated in this connection. The amount of work to be done as expressed by the amount of CO_2 given off is a constant. Experiments at variable temperatures, or at higher or lower humidities than those referred to, as will be shown in Chapter XV, are characterized by more rapid metabolism and would complete the pupal stage or the egg stage in a shorter time. Hence the effect of one degree for one hour or the developmental unit discussed on p. 192 would be characterized by more work, a greater CO_2 production, or in other words the *developmental unit* is *larger*. Hence *fewer of them are required to make up the total energy output of the stage*. This is the justification for using a smaller number of developmental units for the completion of a stage under such conditions.

Recently Northrup (627) has studied a race of inbred aseptically reared *Drosophila* and found that the amount of CO_2 is not a con-

ant for larval life or adult life, but the amount of activity was not easured. This is essential. The total amount decreases as the mperature is raised, which suggests an acclimation process in ock adapted to constant temperatures. The temperatures used, z., 15°, 26°, and 30°, should be within the straight-line limits, and e data of time fall approximately into a straight line, regardless of e variation in CO_2 given off in the case of the larvae.

The product of time and temperature is 100.5 (15°), 98.8 (26°) and)6.4 (30°) which is not a serious deviation, though the number of mperatures is small. This indicates that the straight-line relation olds good on the basis of time regardless of CO_2 relations. Such ecialized organisms can hardly be expected to behave as do those ving in a wild state.

TABLE 14

Total CO_2 produced by Tenebrio molitor during pupal life

DEGREES CENTIGRADE*	LITERS OF CO_2 PER KILOGRAM
32.70	59.30
27.25	58.00
23.65	59.10
20.90	59.60
18.80	
Average..........................	59.00

* One medial degree corresponds to 23.6 cc. of CO_2.

4. Alpha—the zero of the hyperbola

On the basis of the partial conformation of the time-temperature ırve to the equilateral hyperbola, the thermal constant, or product time and temperature within the range which conforms to the uilateral hyperbola, is used. This makes partial use of the old ncept back of summing of temperature. Given the time to comete a stage of the life history, the time to complete an amount of ork, or the time to travel a certain distance, the first procedure is to id the reciprocals of the time (e.g., to complete the amount of ork), and plot them on their respective temperatures. The reciprols of the times which fall in the limits of the equilateral hyperbola ll fall in a straight line. The prolongation of this straight line ts the temperature axis at a temperature approximating alpha

(see curve R, fig. 73A). Reibisch (720) definitely used this as the threshold and Johansen and Krogh found it incorrect (445).

This alpha value may be assumed and adjusted to more accurately by the Oettingen method (629), as shown in table 15, where differences in degrees instead of 0.1 degrees are used to show the method. When the alpha chosen is too low the values become smaller from low to high temperatures, and when too large they become larger from low to high. The values outside the straight-line limits are discordant.

The value of the constant may also be roughly ascertained by multiplying the reciprocal by $\frac{\tan 45°}{\tan \theta R}$, θ R being the angle of the

TABLE 15

Determination of the alpha value by the Oettingen method

TEMPERATURE	HOURS	13° ALPHA PRODUCT	11° ALPHA PRODUCT	15° ALPHA PRODUCT
°C.				
13	1300.0	0	2600.0	−2600.0
16	833.3	2499.0+	4166.0	833.0
18	500.0	2500.0	3500.0	1500.0
23	250.0	2500.0	3000.0	2000.0
28	166.6	2499.0+	2832.0	2165.0
33	133.3	2666.0+	2926.0	2399.0

reciprocal curve. Thus, in curve A of figure 73, tan 45° is 1.00, tan θ R (1000) is 0.400 or $\left(\frac{6}{28-13}\right)$. Hence the constant is approximately 2500, which should be essentially correct as a starting point for the consideration of actual weather conditions.

5. Threshold for temperature and the velocity curve just above it

The temperature threshold (431, 901) is that temperature just above which the rate of development begins to become perceptible. The term was probably first used by the psychologists to express the idea of the smallest stimulus which is perceptible or which gives any reaction. In very careful modern work in determining the threshold of stimulation, it has been observed that just above the threshold the sensation or reaction does not appear every time. Furthermore, the threshold varies somewhat with the condition of the organism.

he concept is entirely correct for the relations of temperature to evelopment. It is not a definite, but rather a somewhat variable oint. Few or no threshold points have been definitely determined. he point marked α on all the graphs has frequently been determined pproximately and use made of it. In all cases this use has led erroneous results. The investigators who have summed mean aily temperatures above alpha have applied the term "zero of evelopment," "critical point," "starting point," to the alpha values. nce the concepts are erroneous, all these terms should be abandoned.

Biology has neglected the threshold concept so much that this ea requires further explanation. Curves for Q_{10} a constant and for rrhenius' formula never reach a zero, whereas activity and develop-ent come to a practical standstill at certain temperatures. The ost important concept is that the threshold is a statistical value. his is shown in one of the few pieces of zoölogical work on the bject (Banta, 57). The momentum of a falling ball at which an pod responds barely, not at all, rarely, and occasionally, may be eraged together as representing the threshold. It will differ with fferent individuals which should also be averaged together to give e species threshold.

Important contributions to the nature of the curve near the reshold have been made by psychologists (431, 901). The formula $= (K \log S) + C$ (R = responses; S = stimulus) has been used some authors in connection with Webber's law. Applied here, is is $V = (K \log T) + C$. V is velocity of development; T is mperature above the threshold, K is a constant factor and C is constant increment. When T is 0, e.g., the threshold velocity is ual to C, and this is a very small quantity, hence 0.001 of a degree-it, hence $V = (K \log T) + 0.001$.

The curve may be drawn and the factor K easily determined, but e curve thus obtained does not ordinarily fit the experimental data ry closely.

Until there has been some thorough investigation of the form of e curve at low temperatures, it is not important to do more than aw a curve that will pass through the data obtained with the best ssible fit.

It is desirable to draw curves according to some definite plan. e following has proven a very useful method (826)

$$y = \frac{x^n}{10} \cdot K \quad \text{or} \quad V = \frac{(T \text{ above threshold})^n}{10} K$$

in which n may be given values of 1.1, 1.2, 1.3, 1.5, 1.6, 1.7, etc. The larger the value of n the greater the curvature. A fit for the experimental data can usually be approximated, and the author is then able to state how he drew the curve.

The obtaining of the data for the lower part of the curve is possible only by indirect means. The closest possible control of temperature is desirable at all points in the lower part of the curve. Variations of more than 0.1°C. should not be tolerated. Development is so slow at the low temperatures that it is not often practicable to bring stages to completion under these conditions. The rate of development may be estimated by rather long exposures at the low temperature followed by exposure at higher temperature. The shortening of the period should be evident. Weese (960) has described a method of computing progress under several conditions. Luce, working in the laboratory of Prof. Chas. Zeleny, has made single transfers of the young stages of *Drosophila* from one temperature to another and states that no stimulation is noticeable (1011).

6. The curve above the straight-line limits

Constant temperature experiments can be run from 2° to 5° above the upper straight-line limit. The movement of individuals into the high temperature procedure may be adopted with rises for short periods into high temperatures. Short exposures may also be used. Up to 40°C. exposures of eight to twelve hours will be possibly compatible with life for many organisms, and many will withstand higher temperatures for shorter periods.

Effects of changes from one temperature to another (95) may interfere with results to a considerable degree, especially as applied to high temperatures. The results of different lengths of exposure of corn to different temperatures were found to be different by Lehenbauer (515) who cites considerable literature. No doubt there are similar results with animals, making it probable that this feature should receive attention. The results of Parker in transferring grasshopper nymphs to lower temperature for sixteen hours per day (Chapman (157)), thus, 27° to 12°; 27° to 22°; 32° to 12°; 32° to 22°; 37° to 12° and 37° to 22°, showed roughly 18 to 30 per cent shorter time than under constant temperature. Under variable temperatures the acceleration is usually 5 to 10 per cent. More recently Cook (206) has moved cutworms from 8° to 12°, 16°, 22°, 27°, and

°C., for different periods of time such as 1, 2, 4, 8, 16, etc. hours
d returned them for the remainder of the day to 8°C. He found
at the eight-hour exposures gave most rapid rate of growth and
eatest CO_2 production. As the time was extended beyond eight
urs the rate fell off rather rapidly to a minimum. Cook also dealt
th various theoretical considerations and constructed a solid model
nilar to that shown by Matisse (585) in his chapter on the same
bject. This model instead of dealing with velocity, temperature
d humidity as suggested by the writer (826) covers temperature,
locity, and time.

No comparisons with outdoor temperatures were carried on and
comparisons were made with variable temperatures which simu-
e normal days. Such comparisons are quite important, for what
desired in climatic work is the knowledge of actual weather and
ily variations. The experiments of Cook and others suggest that
rate of daily rise and fall of temperature may have effects on
rate of development.

IV. PRACTICAL APPLICATIONS—DEVELOPMENTAL UNITS

The ecologist usually is bound to seek the application of experi-
ntal results and theories to the explanation of the phenomena of
ganisms occurring in nature. It is necessary to stick rather closely
the essential facts regarding temperature relations. It essentially
mpracticable to apply the various theories of those who insist that
relations to temperature must follow the laws governing simple
emical reaction, as this viewpoint often outweighs obvious facts
d the attempts at theoretical explanation are almost acrobatic.
must be recognized that with the present limited knowledge
ative to metabolism, scores of mathematical relations can be
nd and theories set forth; even with good physical data two or
ee mathematical explanations can be found.

1. *Developmental units under constant temperatures*

The range of temperature within which the velocity curve for any
ganism's development or activity conforms to the equilateral
perbola may be called *medial* temperatures. The increase in rate
hin this range is proportional to the increase in temperature.
e additional degree in this range means a definite amount of

additional development. Under constant temperatures and with other factors held constant or disregarded, the developmental unit is the difference in amount of development taking place in one hour at a given medial temperature and at another medial temperature one degree higher, as shown by the time to complete the stage (Shelford (825–826)). This unit is better reserved for use in connection with actual weather conditions, as stated in Chapter XV, but it is introduced here to avoid confusion and to illustrate the method of developing such units.

Velocity of development is the number of developmental units per hour. Relative velocity is the reciprocal of time to complete a definite process.

The threshold of development is that intensity or amount of any factor immediately above which development begins to be perceptible in amount.

The developmental total is the sum of developmental units at the time of the completion of a stage or life history or a certain amount of activity.

2. Variable temperatures and the completion of the velocity curve within life limits

The *crucial* variable temperature experiments must be done with minimal medial temperatures occurring at night, and with temperatures rising to maximal medial during the day (see fig. 126, Chapter XI, p. 276). These experiments will usually show an acceleration of development as compared with constant temperatures of the same numerical value as the mean of hourly readings of the variable temperatures. In the codling moth pupa the acceleration amounted to 7 per cent, as shown by a decrease in the developmental total. On the basis of further analysis such as is shown in Chapter XI, this amount of acceleration appears to hold throughout the series of studies on the codling moth. In completing the curve above and below medial temperatures, the developmental *unit* must be used, together with the developmental *total*.

The symbols in figure 73, *A*, represent the data of Krogh (499) on the pupae of *Tenebrio molitor*. This, probably the most careful work yet done, throws doubt on the suggestion sometimes made that no portion of the velocity curve is a straight line. For the straight line portion (18° to 29°) the old law that time multiplied by

nperature gives a constant (2500) holds good; outside of these iits it does *not* hold good, and a day in our latitude hardly passes in iich one or the other of the limits is not exceeded. However, a ;al of 2500 (hour-degree) *developmental units* completes the pupal ige.

The alpha temperature is ascertained graphically in curve *R*, ure 73, in which the reciprocals of time are multiplied by 1000. iis point (13°) has a purely mathematical significance, and hence e Greek letter α is used to designate it. In figure 73, *B*, the hypo- etical curve used by those who sum temperatures, it will be noted at the number of degrees above α (13°) equals the number of de- lopmental units. If this hypothetical relationship were true, velopmental units or degrees of temperature could be summed with actly the same results.

The solid curve in figure 73, *A*, represents the number of units complished in one hour at the various temperatures. Taking °C., for example, the velocity as read from the curve is 10 units r hour. Dividing 2500 by 10 indicates that development can be mpleted in 250 hours at a constant temperature of 23°. At 13° vo developmental units are accomplished in 1 hour and 1250 hours ill be required to complete development. This α temperature is e threshold which would be assumed in "summing temperatures," ı the assumption that development would never be completed at °C. Since development is very slow at the low temperature and ıce organisms will not withstand the higher temperatures con- ıuously, temperatures varying into this temperature range at oout the rate of normal daily rise and fall out of doors may be used check the results of moving animals into and out of these con- tions for short periods of time.

V. SURVIVAL

Survival of animals at high and low temperature is important in etermining the *abundance* following cold winters and hence a subject r experimental attack. Sanderson has studied the winter death ıte of the larvae of the brown tail moth and found temperature om −41°C. to −29°C. are fatal to the hibernating larvae. He viewed the literature (771) on the effects of low temperatures ı winter survival. Shreve (839) has discussed similar relations for ants. Minimum temperatures should be investigated experi- entally with reference to survival.

VI. FITTING CURVES TO VARIABLE TEMPERATURES

The fitting of the curves to variable temperature experiments and outdoor conditions consists in comparing the actual time with the theoretical or calculated time (see table 16). Since the calculation to complete 2500 developmental units is inconveniently long, let us suppose, for the purpose of illustration, that some definite part of the pupal life requiring 90 developmental units was completed

TABLE 16

Developmental units per unit of time (hour) for the development of the pupa of Tenebrio molitor, based upon empirical extensions beyond the data of Krogh. See fig. 74.

°C.	V_1	V_2	V_3	°C.	V_1	V_2	V_3	°C.	V_1	V_2	V_3
−3	0	0	0	15	3.0	3.4	3.2	33	18.3	18.0	18.0
−2	0	0	0	16	3.6	3.8	3.7	34	17.8	17.0	16.0
−1	0	0	0	17	4.2	4.4	4.3	35	17.0	15.0	13.0
0	0	0	0	18	5.0	5.0	5.0	36	15.4	12.7	9.8
1	0	0	0	19	6.0	6.0	6.0	37	14.2	10.4	6.4
2	0	0	0	20	7.0	7.0	7.0	38	13.0	8.6	3.4
3	0	0	0	21	8.0	8.0	8.0	39	11.4	6.4	1.0
4	0	0	0	22	9.0	9.0	9.0	40	10.0	4.0	0
5	0	0	0	23	10.0	10.0	10.0	41	8.6	2.0	0
6	0	0	0	24	11.0	11.0	11.0	42	7.3	0.7	0
7	0	0.3	0	25	12.0	12.0	12.0	43	6.0	0	0
8	0	0.6	0.2	26	13.0	13.0	13.0	44	4.6	0	0
9	0	0.8	0.4	27	14.0	14.0	14.0	45	3.2	0	0
10	0	1.1	0.9	28	15.0	15.0	15.0	46	2.4	0	0
11	0.6	1.5	1.2	29	16.0	16.0	16.0	47	1.6	0	0
12	1.2	1.9	1.7	30	17.0	17.0	17.0	48	0.8	0	0
13	1.8	2.4	2.0	31	17.8	17.8	17.8	49	0.4	0	0
14	2.4	2.6	2.8	32	18.2	18.2	18.2	50	0	0	0

between 10:00 and 11:00 a.m. on April 16 by the *Tenebrio* pupae which pupated April 12 at noon. The velocities in table 16 are written as transcribed from curves V_1, V_2, and V_3, figure 74, opposite the mean (hourly) temperatures for the hour preceding. Since these are units per hour they may be summed for the different hours to give the total for the day. Table 17 shows that with values from curve V_1, the total of 90 is reached at 4:00 a.m. on the 17th, whereas the process was completed at 10:00 a.m. on the 16th, making eighteen hours difference between the theoretical and actual time.

When values from curve V_2 are used (table 18) a total of 90 units reached at a little past 10:00 a.m. on the 16th. This is the hour actual completion as recorded. Curve V_3 would give completion 4:00 p.m., which would be six hours too late. Mere coincidence agreement with one set of variations does not indicate that the rve is the best that may be secured, but a number of such trials ould be regarded as supplying evidence as to the correct curve.

Using table 18, which covers a period of hot summer weather, the per part of the curve may be tested in the same manner as the ver. Ninety units are required and the development in question

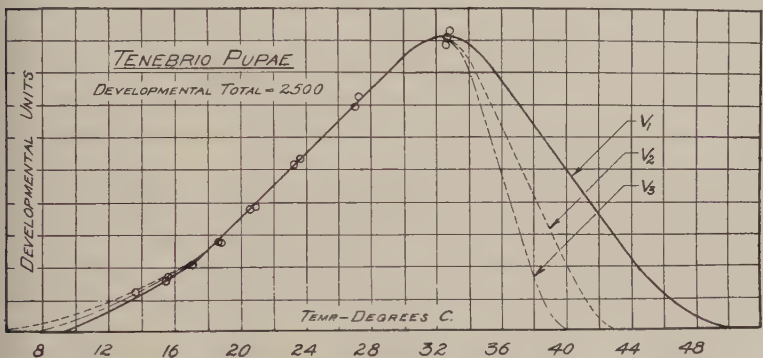


FIG. 74. Empirical extension of the velocity curve beyond Krogh's (499) ta on *Tenebrio molitor* for testing with actual weather data. At the low nperatures; V_1 is drawn on 9.3° as a threshold, $y = \frac{x^{1.5}}{10}$ (1.8); V_2 is drawn on as a threshold, $y = \frac{x^{1.5}}{10}(1.5)$; V_3 is drawn on 7.8° as a threshold, $y =$ (2.1).

completed at 7:30 p.m. on the 25th by individuals pupating at on on the same day. Curve V_1 gives 90 units at 6:15 p.m.; V_2 ves 90 units at 6:45 p.m. and V_3 at 7:30, and with a sufficient mber of checks V_3 would be assumed to be the correct curve. e small difference in time under such weather conditions would nount to considerable under actual long stages.

The method of establishing curves for velocity involves humidity the case of most non-aquatic, free-living animals, and the addinal methods for this are given in Chapter XI.

TABLE 17

Approximately hourly mean temperatures for an Illinois locality in 1917

APRIL 12					APRIL 13					APRIL 14					APRIL 15					APRIL 16				
p.m.	°C.	V_1	V_2	V_3	p.m.	°C.	V_1	V_2	V_3	p.m.	°C.	V_1	V_2	V_3	p.m.	°C.	V_1	V_2	V_3	p.m.	°C.	V_1	V_2	V_3
1	15	3.0	3.4	3.2	1	8	0	0.6	0.2	1	13	1.8	2.4	2.0	1	15	3.0	3.4	3.2	1	14	2.4	2.6	2.8
2	16	3.6	3.8	3.7	2	8	0	0.6	0.2	2	13	1.8	2.4	2.0	2	16	3.6	3.8	3.7	2	15	3.0	3.4	3.2
3	15	3.0	3.4	3.2	3	8	0	0.6	0.2	3	13	1.8	2.4	2.0	3	16	3.6	3.8	3.7	3	16	3.6	3.8	3.7
4	14	2.4	2.6	2.8	4	9	0	0	0.4	4	13	1.8	2.4	2.0	4	15	3.0	3.4	3.2	4	16	3.6	3.8	3.7
5	14	2.4	2.6	2.8	5	8	0	0.6	0.2	5	12	1.2	1.9	1.7	5	14	2.4	2.6	2.8	5	15	3.0	3.4	3.2
6	13	1.8	2.4	2.0	6	7	0	0.3	0	6	11	0.6	1.5	1.2	6	13	1.8	2.4	2.0	6	15	3.0	3.4	3.2
7	10	0.2	1.1	0.9	7	5	0	0	0	7	10	0.2	1.1	0.9	7	12	1.2	1.9	1.7	7	13	1.8	2.4	2.0
8	7	0	0.3	0	8	3	0	0	0	8	9	0	0.6	0.2	8	11	0.6	1.5	1.2	8	12	1.2	1.9	1.7
9	5	0	0	0	9	2	0	0	0	9	9	0	0.8	0.4	9	11	0.6	1.5	1.2	9	12	1.2	1.9	1.7
10	3	0	0	0	10	1	0	0	0	10	8	0	0.6	0.2	10	11	0.6	1.5	1.2	10	12	1.2	1.9	1.7
11	2	0	0	0	11	1	0	0	0	11	7	0	0.3	0	11	10	0.2	1.1	0.9	11	11	0.6	1.5	1.2
12	2	0	0	0	12	1	0	0	0	12	7	0	0.3	0	12	9	0	0.8	0.4	12	10	0.2	1.1	0.9
1	2	0	0	0	1	0	0	0	0	1	7	0	0.3	0	1	9	0	0.8	0.4	1	10	0.2	1.1	0.9
2	2	0	0	0	2	−2	0	0	0	2	6	0	0	0	2	8	0	0.6	0.2	2	11	0.6	1.5	1.2
3	2	0	0	0	3	−3	0	0	0	3	4	0	0	0	3	7	0	0.3	0	3	11	0.6	1.5	1.2
4	1	0	0	0	4	−3	0	0	0	4	3	0	0	0	4	7	0	0.3	0	4	11	0.6	1.5	1.2
5	0	0	0	0	5	−4	0	0	0	5	3	0	0	0	5	7	0	0.3	0	5	11	0.6	1.5	1.2
6	−1	0	0	0	6	−4	0	0	0	6	3	0	0	0	6	7	0	0.3	0	6	11	0.6	1.5	1.2
7	0	0	0	0	7	−1	0	0	0	7	6	0	0	0	7	8	0	0.6	0.2	7	14	2.4	2.6	2.8
8	0	0	0	0	8	2	0	0	0	8	9	0	0.8	0.4	8	9	0	0.8	0.4	8	17	4.2	4.4	4.3
9	2	0	0	0	9	5	0	0	0	9	12	1.2	1.9	1.7	9	11	0.6	1.5	1.2	9	19	6.0	6.0	6.0
10	4	0	0	0	10	8	0	0.6	0.2	10	14	2.4	2.6	2.8	10	13	1.8	2.4	2.0	10	22	9.0	9.0	9.0
11	5	0	0	0	11	9	0	0.8	0.4	11	15	3.0	3.4	3.2	11	13	1.8	2.4	2.0	11	24	11.0	11.0	11.0
12	6	0	0	0	12	11	0.6	1.5	1.2	12	16	3.6	3.8	3.7	12	14	2.4	2.6	2.8	12	26	13.0	13.0	13.0
Total..		16.4	19.6	18.6			0.6	6.4	3.0			19.4	29.5	22.4			26.4	40.6	34.4			72.6	85.7	82.0

Approximate mean hourly temperatures at an Illinois locality in 1916

JULY 25 (1:00 P.M., 12:00 M. 26TH)					JULY 26					JULY 27					JULY 28					JULY 29				
Hour	°C.	V_1	V_2	V_3	Hour	°C.	V_1	V_2	V_3	Hour	°C.	V_1	V_2	V_3	Hour	°C.	V_1	V_2	V_3	Hour	°C.	V_1	V_2	V_3
1	36	15.4	12.7	9.8	1	36	15.4	12.7	9.8	1	37	14.2	10.4	6.4	1	36	15.4	12.7	9.8	1	36	15.4	12.7	9.8
2	36	15.4	12.7	9.8	2	36	15.4	12.7	9.8	2	37	14.2	10.4	6.4	2	36	15.4	12.7	9.8	2	37	14.2	10.4	6.4
3	35	17.0	15.0	13.0	3	35	17.0	15.0	13.0	3	37	14.2	10.4	6.4	3	36	15.4	12.7	9.8	3	36	15.4	12.7	9.8
4	35	17.0	15.0	13.0	4	34	17.8	17.0	16.0	4	37	14.2	10.4	6.4	4	36	15.4	12.7	9.8	4	36	15.4	12.7	9.8
5	29	16.0	16.0	16.0	5	32	18.2	18.2	18.2	5	35	17.0	15.0	13.0	5	34	17.8	17.0	16.0	5	34	17.8	17.0	16.0
6	29	16.0	16.0	16.0	6	31	17.8	17.8	17.8	6	33	18.3	18.0	18.0	6	33	18.3	18.0	18.0	6	32	18.2	18.2	18.2
7	26	13.0	13.0	13.0	7	30	17.0	17.0	17.0	7	30	17.0	17.0	17.0	7	32	18.2	18.2	18.2	7	30	17.0	17.0	17.0
8	25	12.0	12.0	12.0	8	29	16.0	16.0	16.0	8	27	14.0	14.0	14.0	8	31	17.8	17.8	17.8	8	28	15.0	15.0	15.0
9	24	11.0	11.0	11.0	9	26	13.0	13.0	13.0	9	26	13.0	13.0	13.0	9	29	16.0	16.0	16.0	9	28	15.0	15.0	15.0
10	24	11.0	11.0	11.0	10	24	11.0	11.0	11.0	10	25	12.0	12.0	12.0	10	26	13.0	13.0	13.0	10	26	13.0	13.0	13.0
11	23	10.0	10.0	10.0	11	24	11.0	11.0	11.0	11	24	11.0	11.0	11.0	11	26	13.0	13.0	13.0	11	25	12.0	12.0	12.0
12	22	9.0	9.0	9.0	12	23	10.0	10.0	10.0	12	24	11.0	11.0	11.0	12	26	13.0	13.0	13.0	12	24	11.0	11.0	11.0
1	21	8.0	8.0	8.0	1	23	10.0	10.0	10.0	1	25	12.0	12.0	12.0	1	25	12.0	12.0	12.0	1	24	11.0	11.0	11.0
2	20	7.0	7.0	7.0	2	22	9.0	9.0	9.0	2	25	12.0	12.0	12.0	2	25	12.0	12.0	12.0	2	24	11.0	11.0	11.0
3	20	7.0	7.0	7.0	3	22	9.0	9.0	9.0	3	23	10.0	10.0	10.0	3	24	11.0	11.0	11.0	3	24	11.0	11.0	11.0
4	21	8.0	8.0	8.0	4	22	9.0	9.0	9.0	4	22	9.0	9.0	9.0	4	24	11.0	11.0	11.0	4	23	10.0	10.0	10.0
5	22	9.0	9.0	9.0	5	23	10.0	10.0	10.0	5	23	10.0	10.0	10.0	5	24	11.0	11.0	11.0	5	24	11.0	11.0	11.0
6	22	9.0	9.0	9.0	6	24	11.0	11.0	11.0	6	23	10.0	10.0	10.0	6	24	11.0	11.0	11.0	6	24	11.0	11.0	11.0
7	26	13.0	13.0	13.0	7	28	15.0	15.0	15.0	7	26	13.0	13.0	13.0	7	27	14.0	14.0	14.0	7	25	12.0	12.0	12.0
8	29	16.0	16.0	16.0	8	31	17.8	17.8	17.8	8	28	15.0	15.0	15.0	8	30	17.0	17.0	17.0	8	26	13.0	13.0	13.0
9	31	17.8	17.8	17.8	9	33	18.3	18.0	18.0	9	31	17.8	17.8	17.8	9	32	18.2	18.2	18.2	9	30	17.0	17.0	17.0
10	33	18.3	18.0	18.0	10	36	15.4	12.7	9.8	10	33	18.3	18.0	18.0	10	34	17.8	17.0	16.0	10	34	17.8	17.0	16.0
11	35	17.0	15.0	13.0	11	36	15.4	12.7	9.8	11	34	17.8	17.0	16.0	11	35	17.0	15.0	13.0	11	34	17.8	17.0	16.0
12	36	15.4	12.7	9.8	12	37	14.2	10.4	6.4	12	35	17.0	15.0	13.0	12	36	15.4	12.7	9.8	12	35	17.0	15.0	13.0

VII. APPENDIX (STRACHEY'S FORMULA)

In working over old data, summing of temperatures is sometimes desirable when only maxima and minima are given. Strachey (866) has formulæ for computing the average day-degrees above a given base temperature in his comprehensive and scholarly treatment of the subject, based upon extensive records. The following simplified formulæ, derived from the same principles, were used by the Illinois State Entomologist's Office (338) for computing sums of temperature above the so-called developmental zero.

a = first minimum, degrees above or below the zero
b = second minimum, degrees above or below the zero
c = maximum, degrees above the zero
x = average day degrees

I. When both minima are at or above the zero

$$x = \frac{a + b + 2c}{4}$$

II. When the first minimum is below the zero

$$x = \frac{b + c}{4} + \frac{c^2}{4(a + c)}$$

III. When the second minimum is below the zero

$$x = \frac{a + c}{4} + \frac{c^2}{4(b + c)}$$

IV. When both minima are below the zero

$$x = \frac{c^2}{4(a + c)} + \frac{c^2}{4(b + c)}$$

CHAPTER VIII

Control and Measurement of Temperature

I. INTRODUCTION

In spite of its importance, temperature has been overemphasized. ne early development of the thermometer, the convenience and se with which it is used, and the relative ease with which temperare is controlled, have undoubtedly led to this mistake. Follow- the lead of the chemists, biological experimenters have usually tempted to establish as nearly constant temperatures as possible, order to relate biological phenomena to physical and chemical vs.

Ecology and climatology, however, are nearly always concerned th variable temperatures and with applications of results to the planation of community phenomena. Constant temperatures do t have the same effect as variable temperatures of the same mean lue. As is stated on pages 192 and 366, the effect of constant nperatures is to retard development. It is possible that a great al could be learned about the effect of constant temperatures if one rked on animals that live in the soil in the tropical rain forests or those parts of the sea subject to less variation. But in temper- regions where most of the problems are problems of some ecoical or economic bearing, concerned with native species, the chief ue of the maintenance of constant temperature is supplementary her than directly concerned with the economic problem at hand. e purpose of this chapter is to indicate some methods by which desired temperature in climate-simulation experiments may be ablished, controlled, and recorded.

SOURCES OF HEAT AND COLD FOR INCUBATORS AND CLIMATE SIMULATION UNITS

'he sources of heat and cold for maintaining the desired tempera- e in units of equipment include electric current, steam, refrigera- , and running water. The utilization of water for cooling is ed upon (a) its retention in pipes buried in the soil, and (b) poration.

1. *Running water*

Running water is commonly used in three ways: (1) sprayed into air ducts to cool or warm and wash the air being forced into controlled units, (2) circulated through coils or water jackets, and (3) sprayed against units exposed to the sun, for cooling a chamber. Between August 16 and September 3, 1917, the University of Illinois water supply varied only from 15.8° to 16.6°C., though there were the usual summer changes in air temperature.

a. Spray methods (provisional). The regular method of heating or cooling by water consists in spraying water into ducts or enclosures through which air is passed as a means of controlling temperatures. See figure 110, page 250.

When the spray method is used with cold water, evaporation is produced which helps to cool the air, and it emerges with an amount of moisture representing saturation at the water temperature. This method is commonly employed in cooling houses and in the Carrier units, and often constitutes a control of both temperature and humidity.

The spraying of greenhouse roofs, the glass sides of cases, with sprayheads, under thermostatic control, is always an undesirable method, one to be avoided, as it has a bad effect upon light conditions. It also necessitates some means of draining away the spray water. It becomes especially undesirable with hard well waters containing iron, because of the fouling of the parts coming in contact with the water. It is always expensive. Where water is clean and cooling capacity limited it may be used during unusually warm periods but should be an emergency method, and spray heads may be installed to cover breakdown but should not be used for other purposes.

b. Tanks, jackets, and coils. Circulation of water through glass-bottom roof tanks on small units is a valuable method of reducing temperature in chambers exposed to the sun, provided the water is clear and has a small salt and iron content. The supply to such tanks may be put under thermostatic control (fig. 177, p. 419). This is, however, ordinarily not a desirable method as it interferes with lighting, especially if the water supply is not clean enough.

Water is sometimes circulated through a water jacket arranged to give a wedge relation to several tanks working at different tempera-

res. It is also employed to secure temperatures lower than the rounding room. Containers may often be placed in running-water uaria in larger vessels and temperature lowered accordingly. All ese methods, while ones to which the experimenter must often ort, are uncertain and are wasteful of water.

The passing of water through coils in connection with fan circula- n has the disadvantage that the water must ordinarily be used in ne quantity and wasted. Water must ordinarily be recirculated. iere air is circulated over coils, some special form of piping with reased surface must be used to secure good results (fig. 75). tomobile radiators are also efficient for this purpose.

2. Refrigeration (567)

Refrigeration is essential in the maintenance of low or even medium nperatures where light must be admitted. The choice of refrigera-

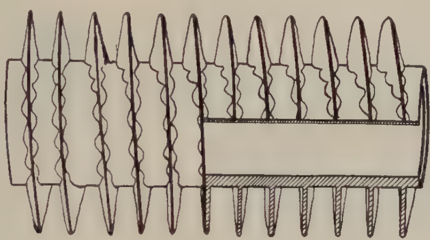


FIG. 75. Aerofin tubing

n machinery is important. (a) The gas (usually ammonia, or sul- ur dioxide) used in the machine must not escape and pollute the nosphere. This rules out many ammonia machines. (b) The eration should be silent and automatic so as to require only occa- nal attention.

Refrigeration is often used directly in cooling, i.e., the compressed rigerant is expanded in pipes in the chamber to be cooled. This , necessary or at least a common practice whenever the tempera- e is to be kept as low as $-40°$ to $-18°$C. ($-40°$ to $0°$F.), as is the e with studies of winter-killing of insect pests and buds. In such ipment unusual care must be taken to prevent leakage of the from the coils used in cooling. Usually, however, some fluid of freezing point is circulated.

. *Machines.* The Audiffren (A–S) and the Carrier machines

(371, 415, 567) and doubtless others, meet the requirements. The former is hermetically sealed; the latter uses a refrigerant which is a liquid at 20°C. and harmless to man. There are many unperfected machines on the market, and also machines cheaper than these, but none should be adopted without a thorough investigation. The former is suitable where a ton or more of ice-making capacity is required daily for cooling circulating brine. The latter is suitable for large requirements. The Frigidaire machine is a good small unit but leakage is easily possible though it very rarely occurs. The "frost coil" is a gas expansion coil but could readily be immersed in brine or water which could be circulated. Cotton (211) used a CO_2 machine.

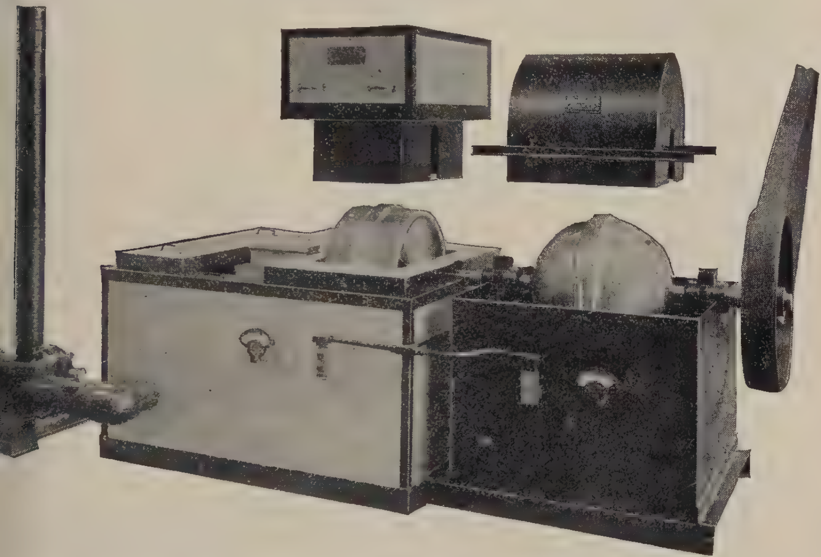
In Audiffren machines (figs. 76 and 77) the internal mechanism of the spherical bell is comparatively simple but ingenious. The com-

FIG. 76. Audiffren rotor or dumb-bell (courtesy of Audiffren Refrigerating Machine Company.)

pressor pistons are moved by the rotation of the outer shell. One of these machines was operated continuously with automatic stopping and starting with changes in brine temperature, for ten years, which is a good record. The cost of the machine is high in proportion to the refrigeration delivered. They have the advantage of being small, so that several units may be required, and hence complete breakdowns are rendered unlikely. Where sufficient refrigeration is needed to demand more than 35 tons of ice per day two Carrier machines (153) of the present minimum size would probably give sufficient refrigeration for the occasional heavy loads and leave a machine in reserve at other times. The Carrier machine is very compact, silent in operation, and under automatic control, but is not made in small sizes.

The Frigidaire machine is practicable for small units but when

ed for biological work should be especially reinforced against akage and the unit placed outside of the chamber where the animals e to be. The Frigidaire machine is automatic and operates by panding SO_2 in a small frost coil. It is suitable in size for ice-xes. This unit, furthermore, can readily be used to give cooling for nall climate simulation units. Figure 78 shows a unit equipped th an enclosed Frigidaire refrigeration outfit. For securing uni-rm temperature in the unit a circulating fan should be installed. small desk fan is suitable for this purpose.



'IG. 77. Audiffren refrigerating machine with covers raised to show "dumb-" in position, condenser tank and circulating pump. Ordinarily for nate simulation a centrifugal pump is used to circulate cooling fluid from brine tank to the unit coils (courtesy of Audiffren Refrigerating Machine npany.)

. *The circulation of refrigerating fluid.* The medium is usually cium chloride solution, though cattle salt has been used. Both to be avoided as corrosive substances and so far as possible non-rosive substances should be sought and used and are in fact under estigation by engineers at the present time. These salts are y destructive of piping and in course of seven to fifteen years ious valves and portions of piping will have to be replaced or per-

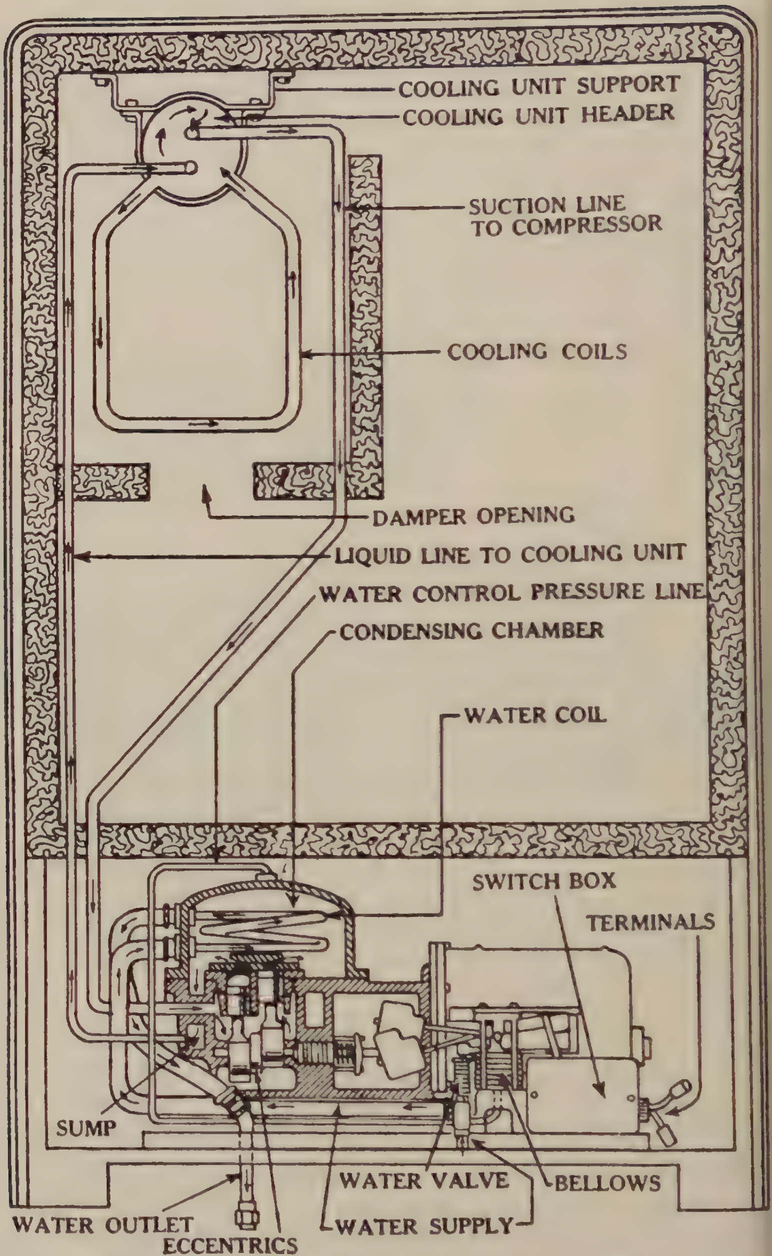


FIG. 78. Diagram of the Frigidaire unit (courtesy of Frigidaire Corporation).

ps the entire system renewed at great expense. The things re-iring attention are:

(1) Provision for continuous pumping.

(2) Provision for by-passing brine to the tank of the machine ıen the resistance in the coils is increased due to the closing of ermostatically operated valves.

(3) Care to provide sufficient fluid to prevent air entering the stem. In the University of Illinois plant where tanks of two ıchines were connected, there was considerable difficulty of this ıd. A tank for an extra supply of fluid is also essential. It may so arranged as to maintain a constant level of fluid in the brine ıks of the refrigerating machine.

(4) Careful installation of piping so as to adjust the resistance rough different coils.

(5) Means of reading and adjusting flow in mains and in coils. e lack of this makes much trouble, certain coils robbing all others.

(6) Means of withdrawing air from coils.

(7) Where refrigeration is limited, means for absolute restriction water cooling coils, which may easily overload the machine.

Pumps and motors for distributing brine should be in duplicate insure circulation at all times. Piston pumps *must not* be used as y introduce air into the brine, which results in stoppage of the ls. Centrifugal pumps are recommended.

The piping for the distribution system should be very carefully nned so as to reduce friction and distribute brine to all coils with- the operation of restricting valves which increase the pressure uired. The installation of such piping, if not given special at-tion, is likely to be left to architectural draftsmen who will make piping conform to the building rather than follow paths best for ıring circulation. The equipment in which refrigeration is to be d should be carefully located. Horizontal branches in parallel the upper floors are to be avoided where a number of units must cooled, as some will rob the others.

n general, troubles with circulation due to air in the cooling fluid y be remedied by the use of centrifugal pumps and supplementary ks to maintain the level of the brine. However, uniform positive ulation may be better maintained where all cooling coils in a ıp are in series; that is, each main group of coils should be in series. e coils in such a system may be opened and closed with three-way

valves, either automatic or manual, and if properly constructed opening and closing will not change the pressure in the main branch. Each main branch should have a flow meter at its point of departure from the general mains. Such a series arrangement with flow meters makes possible regulation of flows in all lines near the pump.

Each coil admits brine at the bottom and discharges it at the top. Air is released from solution by the warming of the brine. A small cock is provided to draw off air and, unless otherwise specified, will point upward and spray brine into the rooms. The vent should turn downward so the brine can be retained by a hose and caught in a

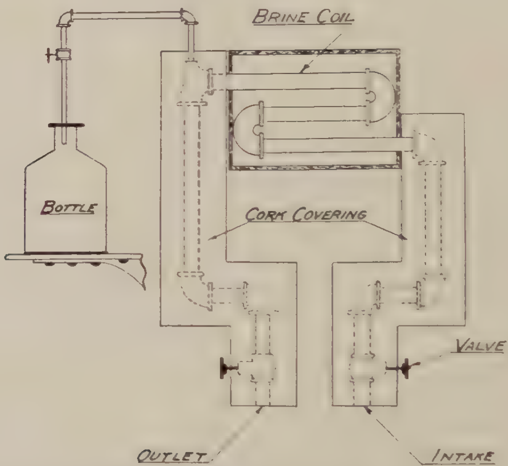


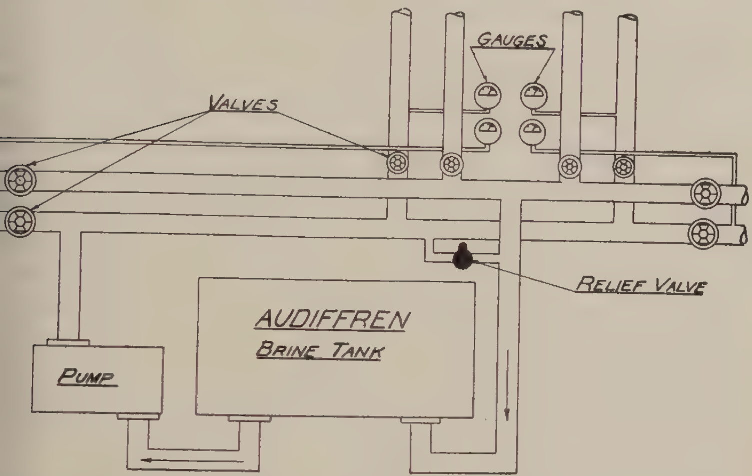
FIG. 79. Diagram of a brine coil and proper form of air relief cock and catch bottle.

bottle for returning to the machine (fig. 79). Air accumulates especially if the overseers do not keep a full supply of brine in the tanks. When the brine falls so that air is occasionally taken in some of the coils commonly become air-clogged and cooling is greatly interfered with.

Where many coils are supplied in different parts of the building the resistance in each branch of the system should be made as nearly the same as possible. In such a system there will usually be some coils that are closed automatically to regulate the temperature. There must accordingly be a relief by-pass which returns brine directly to the tank when the pressure in the line is increased (fig. 80).

Flow-meters and indicators. The standard methods for deter-ing the quantity of liquid flowing through a pipe are: (1). ven- meters, (2) orifice meters, (3) differential manometers and (4) ssure gauges.

n each of these methods the principle involved is a pressure change ch is measured directly on a manometer. This pressure drop is



G. 80. Diagram showing the mains and four branch lines as used at the ersity of Illinois Vivarium, with location of gauge connections and valves gulate distribution of brine to various parts.

. 81. The interior of a Venturi meter (courtesy of Builders Iron Foundry)

tly proportional to the quantity of liquid flowing and in con-ion with a suitable scale is used to give quantities directly.

e venturi meter is a very reliable piece of apparatus, but must ell constructed. It is very costly either to buy or to make, and his reason is less desirable than the orifice meter. When well

designed and well finished, it is accurate to within 2 per cent. It is unreliable, however, in the case of pulsating flow.

Venturi meters are frequently used for determining brine circulation. Figure 81 shows the principle of the venturi meter. The reduced pressure at the constriction is utilized in comparison with the pressure in the main. The venturi manometer shows the flow at any time. Recording venturi meters are available.

The sharp-edged circular orifice is accurate and reliable. It is very easy to make, and at the same time less expensive than the venturi meter. A circular orifice three-fourths the diameter of the pipe (2 inch pipe) is suitable for measuring brine flows. It consists of a monell metal diaphragm set in a flange union. The principle involved is illustrated in figure 107, page 241. Four 1 mm. holes, two on each side of the diaphragm, connect with a low reading differential gauge, and indicate very large flows and variations in the same. This orifice is accurate for quantities up to 140 kgm. per minute.

The pressure of a liquid flowing along a horizontal pipe is constantly diminishing due to friction losses, etc., in the pipe. This loss is proportional, for similar and equal pipes, to the square of the velocity, provided the temperature remains nearly constant. If, therefore, we install a manometer across the inlet and outlet pipe of a coil or series of coils, the reading will be proportional to the velocity and hence to the quantity flowing. This method has been used to determine the quantity of liquid flowing through a short length of straight pipe of small bore. If all that is necessary is a flow indicator, and each of the circuits are approximately equal in every respect, or if they are so calibrated that a known reading may be associated with the correct operation of both, there is no reason why this method would not be satisfactory though it has not been tried out.

At the University of Illinois the various branches from the mains were originally provided with gate valves. It was found that pressure was distributed to the various parts of the building with much irregularity and difficulty. Pressure gauges were later attached in the supply pipes on the coil side of gate valves. The valves were first set so that all the pressures on the coil side of the valve read the same. The valves to certain coils were opened or closed to give the required circulation in the various parts of the system (fig. 80). However, the use of more accurate methods at the main branchings near the machines, so that service men may distribute the pres-

re properly, is advised. Gauges and manometers at the various ils are also essential for the investigator. When water is cooled, re must be exercised not to overload the refrigeration machines.

d. Supplementary systems. Wherever temperatures below freez- g are not required, it is *undesirable* to use brine even though brine ıst be used in the main system. Corrosion of pipes may be re- ced by using water containing a little glycerine, alcohol, or sugar · margin of safety. This should be used in a supplementary sys- n. A brine coil under thermostatic control should be immersed a tank of the water to be circulated. A fluid just above freezing nperature does not freeze ice on a cooling coil. With increased face, as in "aerofin," the efficiency is very much greater, and a culating medium above freezing will do better work than a brine −10°C. in ordinary pipes covered with ice.

Where small coils for cooling bottles and other small surfaces or dies are desired, a small supplementary system may be used. A ermostatically controlled coil from the main circulating system y be immersed in a tank of water or low freezing point mixture d a very small circulating pump used. A very small centrifugal mp may be used and a positive uniform circulation maintained.

3. Heating

Hot water or steam may be used in increased surface coils to heat circulated through them. In general, such coils should be outside unit heated, so that after the supply of steam or hot water is cut that remaining in the coil will not warm the chamber too much. either of these is used it is best to force or recirculate air over m and have them located outside the chamber to be warmed.

Electric heaters are quite satisfactory as they cool quickly after thermostat turns off the current.

III. CONTROL OF TEMPERATURE (150–153)

Methods and devices for controlling and maintaining desired nperature conditions, particularly constant temperatures, are y numerous. Nearly every laboratory worker, incubator manu- turer, and house-heat control engineer has his pet type of thermo- t. It is useless to attempt to discuss the merits of the various es, but there are certain general principles relative to the action hermostats which deserve attention.

1. *Thermostats* (479)

Instability. Many of the cheaper types of thermostats do not operate at the same temperature all the time. Some of them show what has been called "creep;" that is, beginning each morning, as the surrounding temperature rises, the thermostat operates at slightly higher temperatures with each action. In course of the forenoon it creeps up 1° or 2°. Such a thermostat is very undesir-

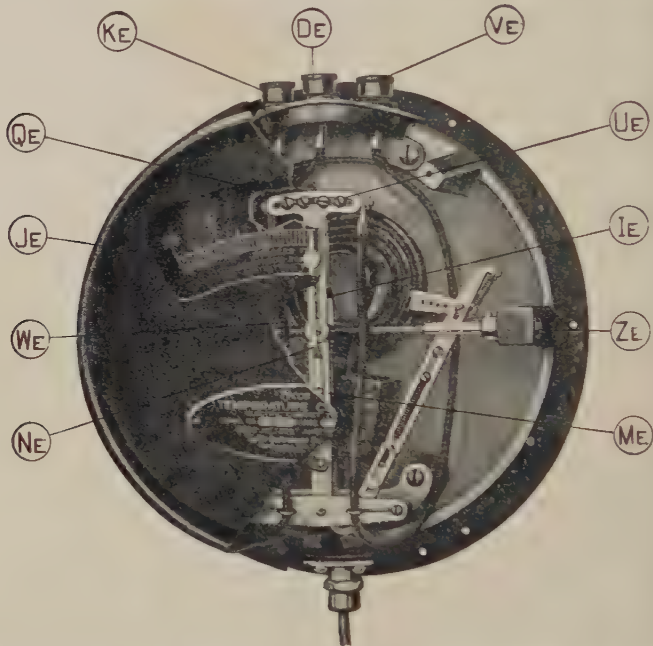


FIG. 82. Tycos electric contact temperature control (courtesy of Taylor Instrument Company. For meaning of letters on the figure, see catalogue, Part 4, p. 65, 1926).

able, but before deciding that a thermostat "creeps" it is necessary to see that the air surrounding it circulates very completely and passes at once into contact with the thermometer used in testing it. Difficulties of this kind, resulting from improper circulation, can of course be remedied.

The second requirement for a thermostat is freedom from change in form and position of the contact points that operate the device. This trouble is most likely to occur in electric thermostats due to burning. The seats on pneumatic thermostats are replaceable.

Thermostats are of two types: those operated by the closing of compressed-air leak port, and those operated by the making of an ectrical contact.

a. Electrical thermostat. One thermostat correct in principle and ery flexible is the *Tycos* mercury-actuated electric-contact thermo- at shown in figure 82. It is based upon the principle of the record- g mercury thermometer. The Bristol Company makes thermo- ats similar in principle.

There are various types of electrical thermostats, but practically one of them can operate successfully when a large heating current asses through the thermostat without relay. A few are provided with ndensers and do not require relays. The DeKhotinsky bimetalic

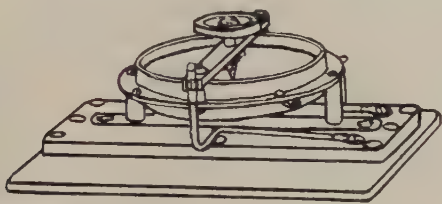


FIG. 83. Chicago Surgical and Electric Company electro-thermostat with ndenser. The principal feature of this thermostat is the diaphragm, which nsists of a hard rubber and a metal disc, riveted together and clamped se- rely around the peripheries, between two special metal rings, the metal disc ing placed on top with a platinum contact attached to same. As the expan- on of hard rubber, when exposed to heat, is much greater than that of metal, e diaphragm becomes warped upward and makes contact and closes the at circuit.

lix type operates without relay up to three amperes. The double sk thermostat consists of two circles, one of vulcanite and one of pper clamped in a heavy metal ring. These operate quite success- lly where a small amount of current is used as in small incubators. ry good results may be expected where the current is one ampere less, if the contacts are kept in first class condition. See Figure 83.

Electric thermostats operating with a relay are numerous, but ne of them require a battery circuit to operate the relay. In ers, a portion of the heating circuit is taken off with a shunt to erate the relay mechanism. For very precise work various in- ument manufacturers will make thermostats to meet particular quirements. The DeKhotinsky, for example, can be made as sitive as desired, and will be supplied with suitable relay by the kers.

As a rule it is better to use thermostats made for commercial work, provided they are sensitive enough and suited to the purpose for which they are to be used. For example the Taylor Instrument Company makes a series of mercury, vapor pressure, and gas actuated thermostats which are calibrated in degrees and which could be made more sensitive for smaller ranges with such alterations as

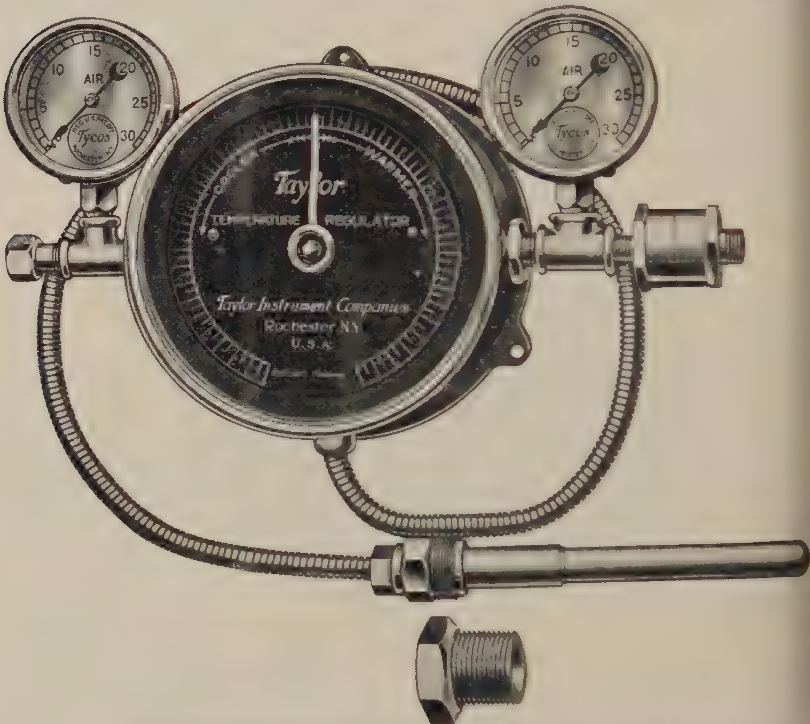
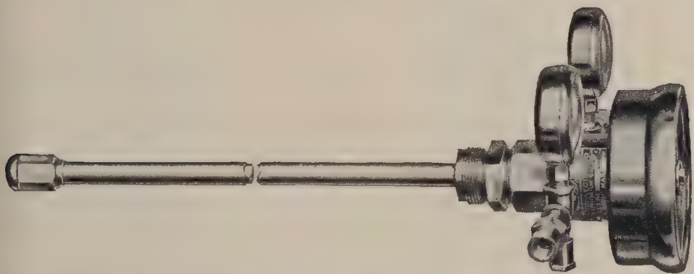


FIG. 84. Tycos air-operated capillary-type temperature regulator (courtesy of Taylor Instrument Companies).

an increase in the size of the mercury chamber, etc. The ranges at which these thermostats will work would permit a reduction to a third and still leave sufficient latitude for biological work. They further make possible the easy shifting of the mercury (or other) bulb to a point where the experiment is actually going on, while mechanisms may be placed on a switchboard These thermostats are made to operate with air and with electric current. The Johnson electric

rmostat in conjunction with a suitable relay operates without eep," and the device has proved successful where very close regu-ion has not been required.

. *Pneumatic thermostats.* Nearly all these operate through the vement of a sensitive part which opens and closes a very minute k port connected with a compressed air system. This leak port nmunicates with a small diaphragm chamber so that, when the k port is closed, the diaphragm chamber fills with air and operates mall valve which connects the compressed air system with the ve chamber of the pneumatic engine which operates the heating ice (see valves, figs. 87–89). The pneumatic thermostat is used pperate numerous devices, namely: to open and close steam valves,



IG. 85. Tycos Type P rigid-stem air thermostat, made up of an outside nding stem and an inside non-expanding stem (courtesy of Taylor Instru-t Companies).

e circulation coils, ventilators and water valves. In fact all s of mechanical movements may be accomplished with these ces. The mechanism closing the leak port may be of any sort. s plan is extensively employed in the control of temperature and lition of air in houses and public buildings of all kinds, and in stry. This has led to quantity production and extensive study lefects and eliminations of defects. A laboratory using air-rolled devices *must* have an *especial* air-treating unit. If clean, air, preferably cooled to $-10°C.$ and filtered, is supplied to these ces, they are not subject to corrosion and other changes in con-ion with the leak port contact. Nearly all trouble is, however, eable to condensation (for removal, see figure 111). In addition arious other uses, air-controlled regulators have the advantage roviding for the development of "intermediate mechanisms"

(fig. 86) which hold a controller in an intermediate position; for example, they may hold a ventilator half open, or a three-way air- or water-valve half open, thus providing for the mixing of two kinds of air or water within the valve without the sharp changes that take place when one valve is closed and the other open.

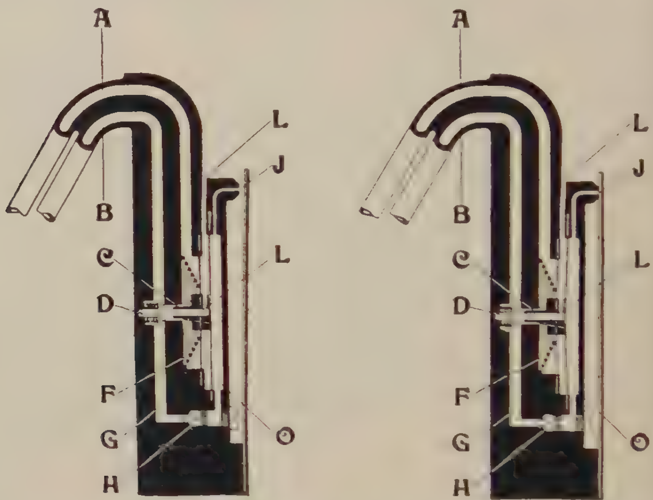


FIG. 86. Johnson intermediate thermostat mechanism. Compressed air is supplied to the thermostat at 15 pounds per square inch through the tube *B*. Another tube, *A*, leads to the diaphragm operating the mixing damper. By filling with or exhausting compressed air from pipe *A* the thermostat operates the diaphragm, back and forth. Passageway *L* on the thermostat is an exhaust port to the free air. Compressed air from *B* is admitted to and exhausted from *A* which leads to a device similar in principle to the three way valve (figure 87) by the valve *D* (open in the left hand figure closed in the right). Compressed air from *B* flows into the chamber *G* and through the restricted opening *H* into chamber *O*. Exhaust port *J* allows the air to escape from chamber *O* faster than it can enter through *H* when the thermostat is in the position shown at left. The right hand figure shows the position of the various parts of the thermostat before the proper temperature is reached. The sizes of openings control the amount of air leaving it, and control the positions of the diaphragms. When *J* is closed the diaphragms are bent to the left as in the right hand figure which closes *C*, which is held open by the spring *F*. Further pressure opens *D* and admits air to *A* and finally to the air chamber of a control mechanism.

Manufacturers construct reverse thermostat mechanisms the operation of which with an ordinary valve (fig. 88) would turn on the heat when it became too warm. These may be used with reverse valves (fig. 89) so that the failure of the air supply will turn

ım off instead of on. The same result may be accomplished by ting a direct acting valve in the supply line and connecting it ctly with the operating air. Electric switches, etc., are also le in reverse form. It is important to use some such form of tection in scientific equipment. Some valves and some air ors are provided with rubber fabric diaphragms, others with per silphons (e.g., Johnson valves). These copper silphons are ranteed for ten years; on radiators in apparatus where the valve ement is every five minutes, the life of the silphon is short, a year or more.

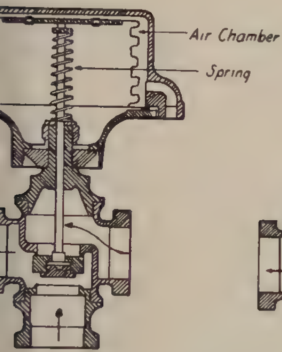


FIG. 87

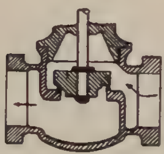


FIG. 88

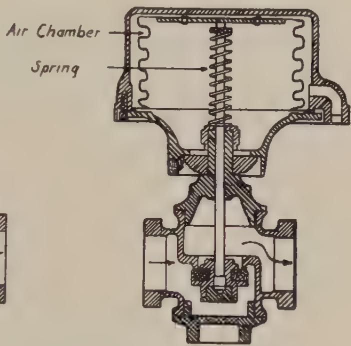


FIG. 89

G. 87. Johnson three way valve, for use with an intermediate pneumatic tive part (see figure 86) to mix air or water of different temperature or dity, etc.
G. 88. A direct acting radiator valve body.
G. 89. A reverse acting valve for use with reverse thermostats with a to prevent overheating if air pressure fails or the silphon diaphragm is red.

eumatic valves are of three types (figs. 87–89): positive action, se action, and intermediate or three-way. Positive action s are the type that is commonly used on radiators and should nployed wherever the continued positive action of the valve not be detrimental to the experiments in hand. However, e steam or hot water is continually turned into the system, cident may result in destruction of the plants or animals under imentation. The occasional rupture of a diaphragm or silphon s and leaves the heating element in operation to the detriment e experiment. The reverse action valves that should be used

under such conditions are more likely to cause the chamber to become too cold, and hence are safer. Valves and other mechanisms operated by solenoids are also available.

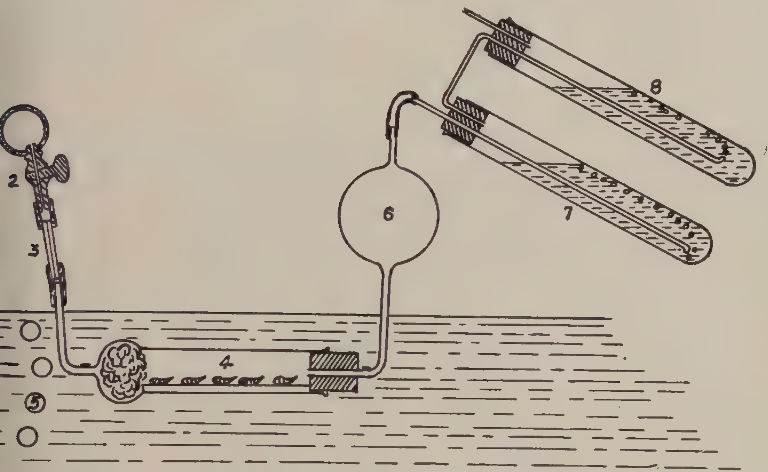
The intermediate three-way valve and intermediate thermostat mechanisms are best adapted to use in mixing air of different humidities, water of different temperatures, etc. They do, however, require more careful adjustment than the positive action devices, but well-constructed types may be graduated so as to set approximately for particular conditions. Air thermostats may be used to operate electric switches (fig. 151, *D*,) and electric thermostats may be used to operate air mechanisms. One of these electric pneumatic devices is the Johnson E. P. valve (fig. 151, *C*, p. 357), which was one of the first mechanisms used in the regulation of temperature in buildings. The Leeds & Northrup recorder mechanism is also used for regulation. The Bristol Company also has thermocouple regulators on the market.

c. Air circulation in chambers under temperature control. It is fairly safe to state that no experimental chamber, large or small, will be of a uniform temperature throughout unless great care is taken to insure very complete circulation of the air within. An incubator 3-foot cube may have a thermostat which is accurate to 0.01°C., but without circulation this temperature is merely maintained at the thermostat. A series of cultures occupying the available shelf space will usually differ from each other as much as 2°, and since most incubators, bacteriologist's type, are not delivered to the purchaser with any means of circulating air, it is necessary to assume that experiments performed in them may have differed as much as 2° in temperature, unless special precautions were taken.

2. Chambers

There are many incubators for chemical and bacteriological work which keep fairly constant temperature at the thermostat. Numerous types with fairly good regulation are without air-stirring fans. Some of these incubators have ice chambers and can be depended upon to maintain temperatures at or below 20°C. Few, if any, of the ordinary incubators for chemical or bacteriological work have any provision for admitting sunlight so as to make conditions suitable for growing food plants, or have any means of artificial lighting for experimental purposes (450).

. *Water baths.* The closest regulation can probably be carried with water baths. Krogh used very simple methods of this kind ɪis work on standard metabolism of Tenebrio and made provision measuring the CO_2 given off as shown in figure 90. The Freas sitive water thermostat (fig. 91) is one of the most valuable in-ɪments for work with small organisms where light is or is not uired. In refined work the selective absorption of light by ɪer must be considered. The thermostat is very sensitive. By cing the equipment in an uninsulated glass tank, diffuse lighting y be secured. As sold on the market this piece of apparatus is



ɪG. 90. Krogh's (499) apparatus for measuring CO_2 output of pupa main-ed at a constant temperature in a water bath.

gned for use in the laboratory, especially where exacting physico-nical experiments are being carried out, requiring absolute con- of all conditions, particularly temperature. The thermostat ntains the temperature for which it is set within 0.002°C. over finite periods of time. The range is from the temperature of room to about 50°C. Refrigeration may be added for lower peratures.

Units requiring refrigeration. While the first suggestion as to ing rooms to be run at low temperatures usually is to recirculate air within the unit, experienced engineers usually avoid that ɪod. Their reasons are as follows:

Cooling capacity within the unit must be large for periods when the surrounding air temperature is high. When the surrounding temperature is low, the unit then becomes too cold.

There must be frequent stopping and starting of circulating fans, which is likely to give motor trouble.

The stopping and starting of the circulating device is likely to give rhythms of temperature.

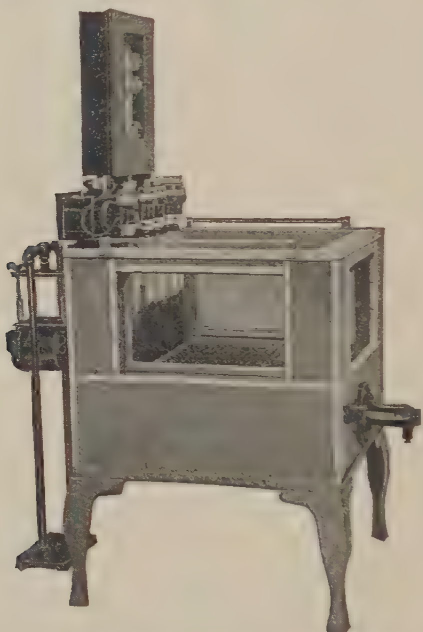


Fig. 91. A Freas sensitive water thermostat. Large size, capacity 340 liters (courtesy of Thermo Electric Instrument Company.)

(1) The Hottes unit. One of the most generally useful laboratory units is the Hottes unit, originally designed by Prof. Chas. F. Hottes of the University of Illinois (fig. 92). It is open to the first two objections stated above, but it admits of modifications to remedy these. For use in a room with temperature control at temperatures to 15° below room temperature, this unit works well with merely a fan-starting thermostat giving a very constant temperature. A small motor with a reverse fan draws air into a galvanized box from the refrigeration coil and forces it upward at one side of a platform

glass, or transite, while it passes down into the coil spaces at the
ner side. The ends of the platform and the box partition (except
the holes) are air tight. It is one of the most generally useful

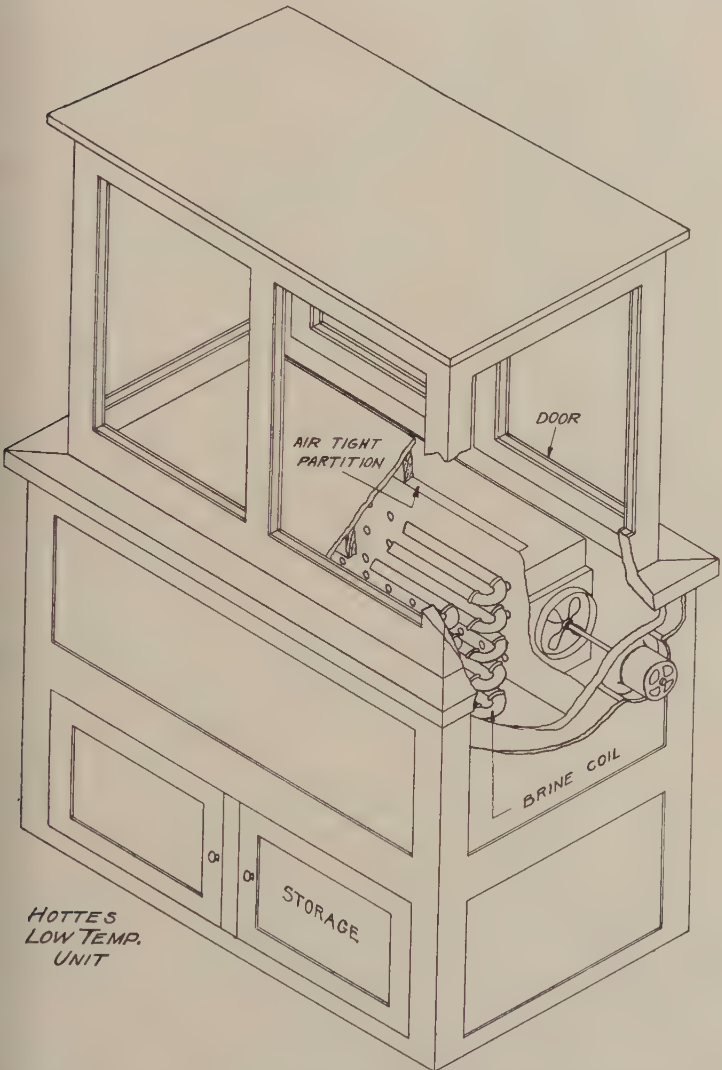


FIG. 92. A Hottes constant low temperature unit with cabinet below

types, evidently suited to the needs of plant physiologists. The unit in the writer's laboratory is very useful for dishes of aquatic organisms. For kinds of work in which it is necessary to look at animals to note progress, the unit is very undesirable because the

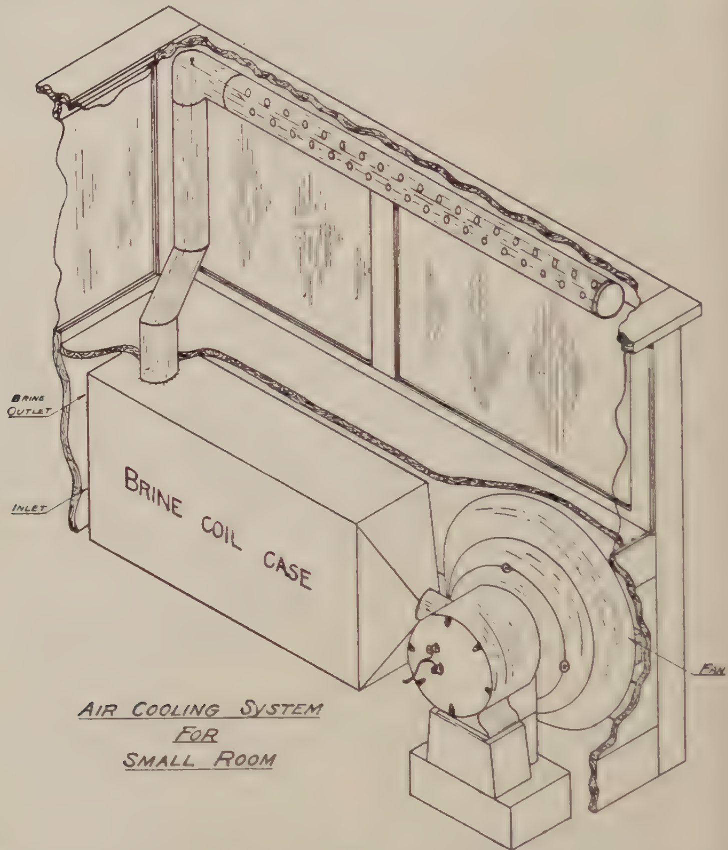


FIG. 93. A duct cooling device which utilizes a refrigeration coil, enclosed in a galvanized-iron air-tight case which is connected with a Buffalo Forge Company's blower fan on one end and with a pipe leading to the top of the side of the chamber to be cooled. This pipe contains a number of half inch holes. The blower draws the air from the lower part of the chamber as shown, passes it over the coils and forces it to the top and out the holes. The operation of the blower was regulated by a Johnson hot water thermostat (Harding and Willard (371), p. 464) which operated a pneumatic switch and turned the current on and off the fan motor in accord with the operation of the thermostat. These thermostats were made to operate within about one-half degree C., making almost a straight line on the ordinary thermograph record sheets.

imals must be removed from the room and hence are warmed. ie unit does not operate well at a temperature just below that of e surrounding room or in rooms such as greenhouses where there is lrop at night, because the unit falls below the desired temperature account of the large cooling surface inside. Additional thermo-ts to stop the brine circulation or turn on heat units are required. . Hottes has overcome these difficulties in his units.

(2) Duct unit. Figure 93 shows a duct recirculating temperature ntrol device used at the University of Illinois. The plan shown ices the blower inside. The thermostat stops and starts the motor-erated blower. Although difficulty resulted from the frequent rting and stopping of the split phase motors, this plan proved quite ccessful, particularly when supplemented with stirring fans to ce care of the inequalities of temperature. If the unit is made gh enough to have the coils below the floor, a differential thermo-t which turns a damper and switches the air partially or wholly o a duct below the shelf instead of the coil chamber, would remedy e difficulty in part and allow the fan to work continuously. Under tain conditions of operation a thermostat outside the unit should used to turn off the brine and turn on the heat. In general, how-er, engineers usually prefer to put the control apparatus outside e unit.

(3) The surrounding room. Rooms in which constant temperature its are housed should be under thermostatic control, and green-uses should be equipped so that they can be held at or a little ow outside temperature during midday peak. The uncooled enhouse is perhaps the greatest menace to accurate work, especi-y in entomological lines.

In the field laboratory of the Department of Horticulture of the iversity of Illinois several large rooms are cooled to freezing or as as −18°C. (30°F. below zero) by direct expansion of carbon xide. These rooms are large enough to hold a considerable quan-y of fruit. Smaller chambers (about 1 meter cube) have been up within these so that a series of five chambers may be run at nstant temperatures from 1 to 3°C. higher than the room in which y are placed.

(4) Temperature control in large chambers. The usual method temperature control in large rooms where constant conditions are uired, consists in moving conditioned air through the chamber

sufficiently fast to maintain the desired temperature and humidity. This is the plan employed in the control of conditions in rooms connected with dwellings, public buildings, and special conditioned operations in industry. This is the method employed by the Carrier Corporation in connection with insect breeding chambers installed at the Kansas Agricultural Experiment Station. This system is quite undesirable for any purpose in which it is necessary to control evaporation because the velocity at which the air moves through the room varies from time to time. There is, however, no objection to this method *for temperature control*, provided animals are placed in containers and the rate of ventilation and the humidity of the small chamber are controlled separately. Where steam is employed for heating the air, such a plan is undesirable because the steam remains hot in the coils for a long time after the desired temperature has been reached and the thermostat has closed the connection between the coil and the steam mains.

(5) Maintenance of constant temperatures over long periods. Professor Zeleny has successfully maintained a temperature of 17°C. and of 27°C. over a period of nearly ten years. The two chambers have continuous circulation of air by means of electric fans. Each is enclosed in a small room supplied with refrigeration and heat and held at a temperature 2° lower than the small chamber. The small room is in a greenhouse with thermostatic control in winter, and spray heads and good ventilation in summer.

c. *Variable temperature apparatus.* Few organisms live under constant temperatures. For most organisms both a daily and a seasonal variation in temperature occurs, which is accompanied by variations in all other conditions. It is, therefore, essential that climate-simulation work should cover the variable conditions; in fact, they are probably more important than the constant ones.

The simulation of the daily march of temperature for any season involves a study of thermometer records over a number of years. It has to be borne in mind that during the first half of the warm season there is a rise of temperature and during the second half a fall in temperature from month to month, and a corresponding reversed trend during the cool season. It is further necessary to note that this rise or fall in temperature is in itself cyclic, though irregularly so. There are cold waves and warm waves and periods of precipitation and evaporation.

(1) Desirable apparatus. Variable temperatures to simulate the erage day may be secured by changing the contact position of a librated thermostat by a rotating cam cut for any desired program d operated by a clock (fig. 94). The Taylor Instrument Comny has developed such an air-operated thermostat as shown in fige 95. However, a cam operating against a spring may be used with y bimetallic two-contract (three-wire) thermostat. These can be ranged so that the longer the radius on the cam the higher the nperature, which makes the visualization of the daily program sy. The great difficulty lies in the calibration of the thermostat

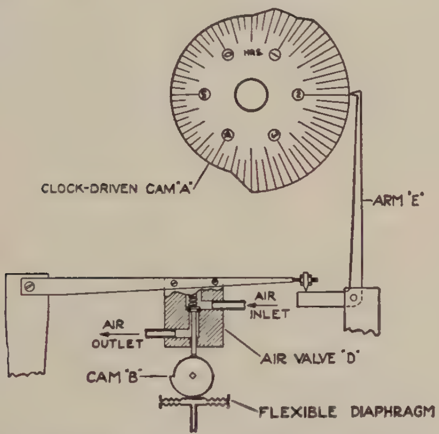


FIG. 94. Tycos "Thermo-Tyme," a program thermostat operated by air l a clock driven cam (A). Change in temperature changes the position of flexible diaphragm and closes or opens an air valve in the regulator which erns the position of the valves controlling the heat (courtesy of Taylor trument Company.)

h reference to the exact temperature and position and the amount movement per degree. Unfortunately, the price of a single Tycos hermo-Tyme" is between $300 and $400.

2) Provisional apparatus. If the sun shone daily it would be a rly simple problem to imitate daily variations in a glass-roofed lding and in glass containers. The temperature in a glass-roofed lding commonly goes 10° higher than the outdoor temperature h the usual greenhouse ventilators open, while a small glass coner is likely to rise 20° higher than the temperature of the glassfed room. Temperatures of 60°C. have been recorded in closed

chambers in a greenhouse with ventilators open and a temperature of 32°C. outside. It is necessary to take such differences into ac-

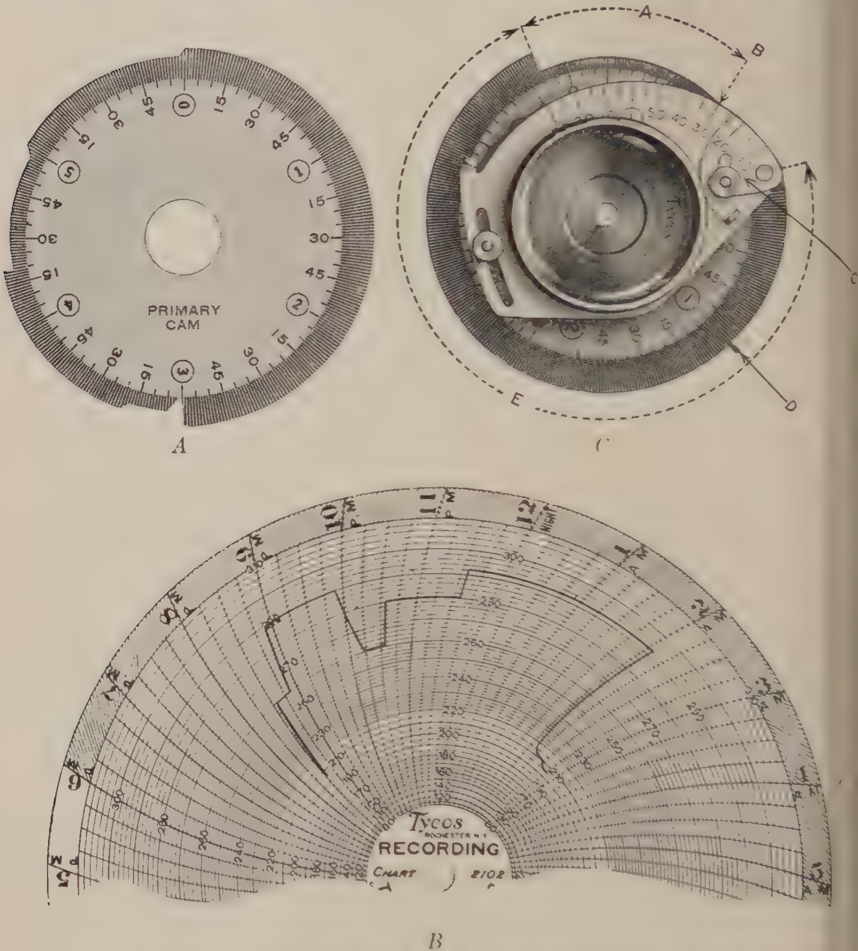
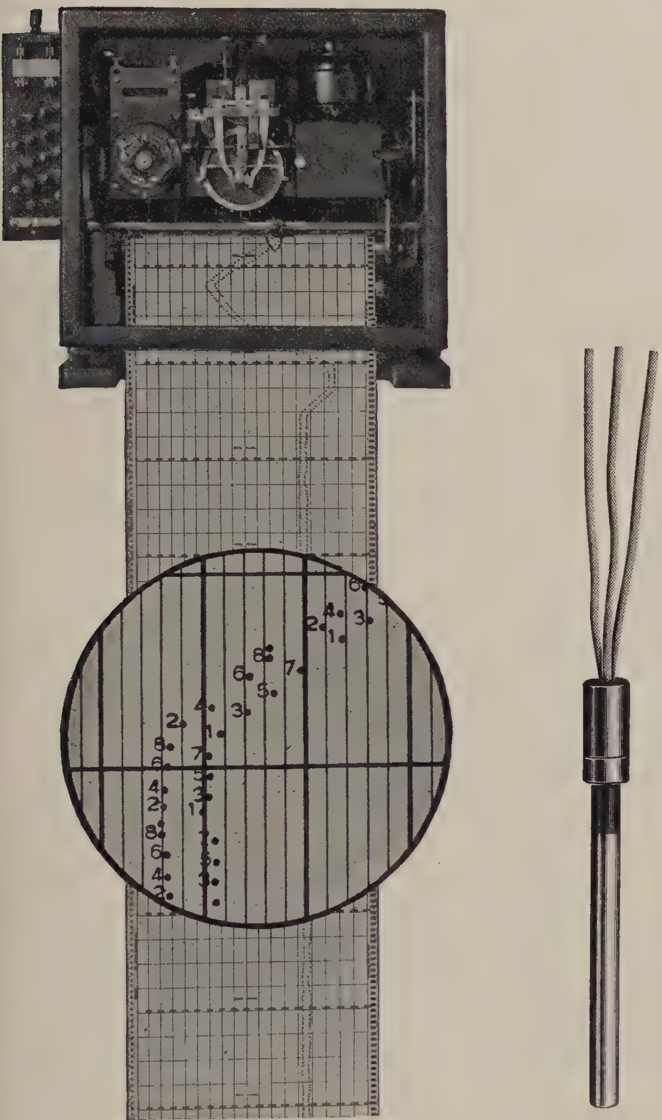


FIG. 95. *A*, clock driven cam cut to give the temperature program shown for the four hours indicated by the chart from a circular thermograph *B*. *C* shows an adjustable cam (courtesy of Taylor Instrument Companies).

count when providing for the control of temperature in glass cages such as are commonly employed in experimental work.

Whenever the sun shines, the simplified temperature day, which



A *B*

Fig. 96. Leeds and Northrup resistance thermometer recorder with a round
e resistance thermometer with three leads which make it independent of
gth of lead and temperature of the intervening space (courtesy of Leeds
Northrup Company.)

consists of the uniform night temperature for about ten hours and the rapid rise to about 2:00 p.m. followed by a fall at about 8:00 p.m., can be obtained in a glass-sided chamber in a greenhouse by merely providing a thermostat which turns on the heat at night and maintains a constant temperature for the ten hours and which closes off when the sun begins heating in the morning. With no means of cooling, the temperature starts to rise as the sun begins to shine, creeps up slowly to the hour stated and then falls off again. Often for a series of days the desired conditions will be obtained without the use of means of keeping the temperature down at mid-day. Such a device is, on the whole, necessary and when installed, consists of a second thermostat which opens a water valve, turning water into a tank above as shown in figure 177, page 419, or starting spray heads as indicated on the same figure. A carefully selected thermostat will turn on the cooling device and maintain the temperature at the desired upper limit during the hot part of the day, turning it off again when the temperature falls below. That is, the device consists of two thermostats operating heat and cold supply at a desired number of degrees apart. The difficulty of such a system arises, however, when because of cloudiness the sun fails to raise the temperature, but this difficulty may be eliminated by the turning on of artificial lights adjacent to the walls of the experimental cage. Every such unit should, of course, be provided with the means of completely circulating the air within the cage.

The manual and sun-produced variable temperatures described above, of necessity vary somewhat with the outside temperature or may be made to do so. They accordingly may be used to compare with the more regular mechanically produced temperatures. It is desirable, however, to imitate natural temperatures in which the mean daily temperature is raised or lowered through a raising or lowering of the entire daily regime. Obviously, there must be either a very special adjustable cam, or the cam must be changed daily. The adjustable cam now on the market (Tycos) is usable to determine the rate of rise of temperature. The position of the cam relative to the contact points may be varied so that the temperature may be raised an average of one degree per day.

There is no doubt, however, that the study of different methods of variation of temperature is a fruitful field and should be undertaken regardless of expense because of its probable importance in actual climatic effects.

IV. RECORDING TEMPERATURE

The continuous recording of temperature is an essential part of reful experimental work. Unfortunately, continuous temperare recording devices have been developed chiefly for meteorological servation or for taking the temperature in rooms. The sensitive rt is quite generally associated with the clock in a metal box. ie device, accordingly, occupies considerable space in a small coniner and the temperature recorded is not the temperature at the int where the animals are but it is the temperature at another int which may differ somewhat. The demand for continuous rerding instruments with insertion bulbs has been so small that they ve not progressed like other types. Most of the recording thermomers that have been developed are round dial devices operating by ock work and requiring a change of sheets every twenty-four hours. ch instruments with insertion bulbs of various forms and of not o large size are made by the Taylor Instrument Company, the xboro Company, and the Bristol Company, as well as many others. me of these instruments are very sensitive and are accordingly luable for certain types of work. The Foxboro and Bristol inuments have an advantage over the Taylor instruments in the ct that they have flexible reinforced extension tubes easily bent o any position.

It is desirable to use instruments that will run a week without ange of sheet, and for most types of work it is not important to ve a record of all slight fluctuations. A Friez soil and water ermograph is adapted to the use of experiments, but the bulb is fortunately large so that it cannot be inserted into a bottle or small ntainer. Otherwise, the device is excellent. It appears that no ention has been given to the developing of a small-bulb eight-day linder-type thermograph either on any of the usual principles or as thermo-couple, or resistance recorder. Instruments could unubtedly be developed which would provide very small bulbs and rmit the experimenter to purchase insertion thermometers in sirable individual units.

Perhaps the best small sensitive parts on the market are the Leeds Northrup resistance thermometers and the thermo-couple thermomers used in connection with their resistance and potentiometer corders. The Leeds & Northrup Recorder, e.g., 16 pt. resistance

recorder, is the most practical instrument for accurate work. Its thermometers are about the size of a lead pencil and half as long.

Their round type of resistance thermometer is ordinarily supplied with the instrument, but the flat type is more sensitive and has less lag. They also make thermocouple recorders with nickle compensators which do away with a cold junction constant temperature.

Among other recorders for straight sheets is the Cambridge-Paul, which makes a tracing on a narrow sheet. The records are accordingly a little easier to follow. The Calendar recorder was one of the early developments of this kind. Several other firms have developed "strip" chart recorders but mainly for high temperatures.

CHAPTER IX

Ventilation Under Experimental Conditions

I. INTRODUCTION

Biological experimentation on animals living in air demands circu- ion of the air through containers to simulate natural conditions, d to maintain humidity at the required point. In the writer's n work, air has been passed through chambers varying from 50,000 50 cc. capacity and at rates varying from 25 to 3,000 cm. per nute. A flexibility is required which can hardly be provided ex- ot by means of compressed air. The air should be as free from dirt d foreign gases as possible. Most air compressors necessitate ntact between the air and either oil or water. Oils are decomposed the pressure and the high temperature occurring in oil-lubricated npressors. These decomposition products are of the nature of ers, any of which may have undesirable physiological effects. water-lubricated compressors it is necessary to take in account the solved content of the water. Most waters will liberate carbon xide and waters from deep wells may contain methane or other minating gas constituents. Most of these gases have physiologi- effects, and the direct use of tap water is usually inadvisable.

II. AIR COMPRESSORS

compressor in which distilled water can be used and renewed n time to time is the most desirable type. These conditions are by the Nash hydro-turbine. The plan of this compressor is wn in figure 97. Figure 98 shows a plan of operation by which same distilled water is recirculated through the compressor. water from the separator drains into the distilled water reser- whence it recirculates to the compressor. Under these condi- s the air discharge is free from moisture droplets and practically rated with moisture at the temperature of the water in the tur- . If the distilled water is renewed from time to time, well- hed air, comparatively free from impurities, can be delivered. frequency with which it is necessary to renew the distilled water

is dependent upon the amount of air used and the amount of dirt and foreign matter in the air. Each operator will have to determine this for his own conditions.

The Nash hydro-turbine is made in several different sizes, the smallest size delivering upward to 25 cubic feet of air per minute and the largest size upward to 250 cubic feet of air per minute. They are furnished direct-connected with suitable motors. The prices are reasonable, and the machines are exceptionally durable.

These compressors will not compress air beyond 14 or 15 pounds per square inch; accordingly, storage tanks and low pressure equip-

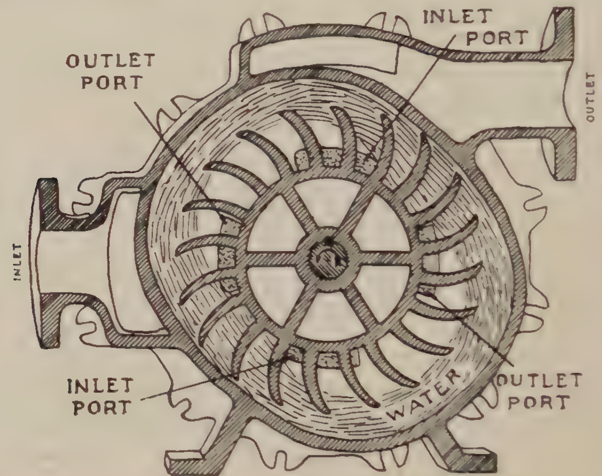
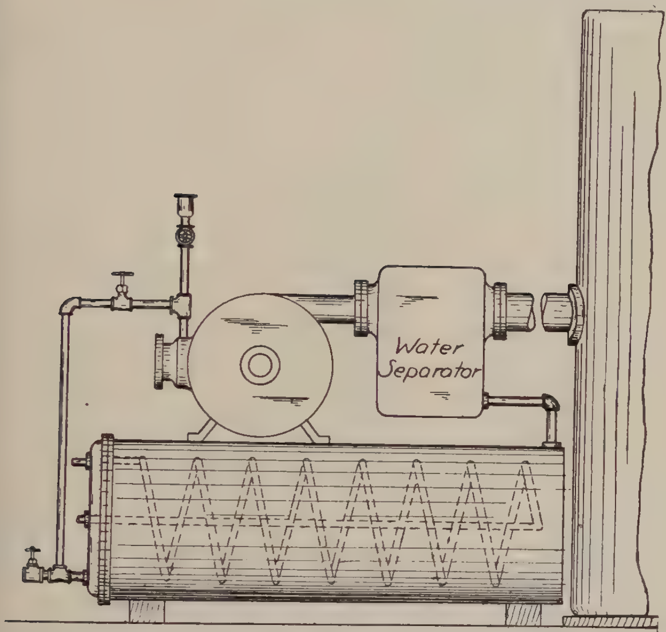


FIG. 97. Cross section showing the principle of operation of the Nash Hytor Pumps.

ment must be used. Mr. F. G. Zinsser of the Zinsser Manufacturing Company states, "They were installed in our plant for the purpose of washing the air which enters one of our rooms, free from dust and reducing the number of bacteria, and for both purposes the machines were perfectly satisfactory."

The storage tank to be used with these low pressure compressors should be roughly ten times the amount of air used per minute with the compressor set to start when the pressure falls to 10 pounds and stop when the pressure rises to about 13 pounds. The amount of air actually used in experiments on insects run in large series to meet

e requirements of testing the effects of different conditions on uni-
rm stock, on a practical scale as experienced in the work of the
inois State Natural History Survey, was about 10 cubic feet per
nute. These experiments were designed to duplicate the actual
tdoor conditions, but other experiments would often involve
ting of varying rapid rates of air movement, so that the amount
uld be more than doubled in figuring on equipment and power,



IG. 98. Air system with distilled water tank below a Nash Hytor with
rator returning distilled water. Cooling coil for distilled water shown
oken lines. The air storage tank is indicated at the right.

pressure equipment of three or four times this capacity is ad-
d to take care of expansion of the plant, inefficient operation,
unexpected conditions.

1. Operating pressure and pressure reduction

or ordinary cage ventilation 3 to 5 pounds pressure is adequate.
s accordingly desirable and frequently necessary to reduce the
age tank pressure with reducing valves that serve also as pressure

regulators to take care of the fluctuation in the storage tank necessary to stop and start the compressor motor. The selection of reducing and regulating valves is of considerable importance. The Mason lever style reducing valve for low pressures is quite generally recommended for this service. The ordinary type of valve, however, appears to have too stiff a diaphragm and does not operate well when the diaphragm chamber contains water. It is, therefore, important in securing valves for this purpose to specify quite exactly the conditions under which they are to be used. The initial and reduced pressures should be given and the liability to fill with water taken into account (fig. 99).

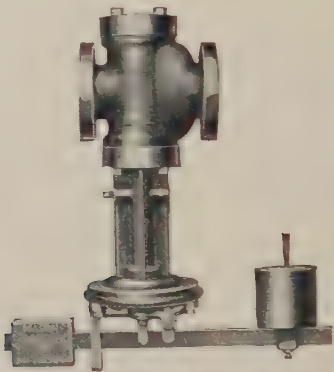


FIG. 99. Showing a Mason regulator of type suitable for reducing low pressure of (15 or 10 pounds) 1050–700 grams per square centimeter to (5 or 3 pounds) 350–210 grams per square centimeter (courtesy of Mason Regulator Company).

2. Central air supplies

There is nothing to be gained by the use of oil compressors. The principal reason, probably, for using them will be found in the existence of an extensive plant for supplying compressed air in the institution in which a climate-simulating plant is to be installed. Such plants are usually provided with oil lubricated piston compressors and usually carry pressures from 50 to 85 pounds in the initial storage tank. The air from such a plant at the University of Illinois was of better quality than would be expected. The compressor intake was located in the engine room of the power plant about 6 feet below the level of the large boilers in the adjacent section of the building. The engineers maintained that the air taken from near

floor would be a better quality than air taken from higher levels ide the building. They based this on the fact that the inflow of from the outside, which supplied the necessary oxygen for the com-tion of much of the coal, was so great that the necessary difference temperature under such conditions rendered the inflow at this nt enormous. Analyses of this air taken at the University of nois Vivarium and Power plant with a large and variable amount CO_2 are shown in table 19. No. 1 and No. 2 samples from pipes he Vivarium; No. 3 sample from pump room in power plant.

Vhile the use of such air is not advised, connection with such a em is desirable for the tiding over of breakdowns of the neces-r equipment; also, for rough work such air may be used to save ense in the early stages of the development of the plant. When 1 air is to be used as a chief supply, a storage tank in the building

TABLE 19

Analysis of compressed air by J. M. Lindgren

CRIPTION SAMPLE	CARBON DIOXIDE	CARBON MONOXIDE	$C_n H_{2n}$	OXYGEN	NITROGEN
	per cent	*per cent*	*per cent*	*per cent*	*per cent*
No. 1	0.31	0.000	0.000	20.92	78.77
No. 2	0.09	0.000	0.000	19.84	80.07
No. 3	0.25	0.000	0.0C0	17.15	80.29

re the apparatus is installed is desirable. It is necessary to use pressure reducing regulating valves such as the Mason reducing e with large diaphragm chamber for pressure below 5 pounds. se valves were used at the University of Illinois in connection the air supplied from the central plant. It was found that it 60 pounds on the high pressure side was necessary to operate e valves and that the air must be freed from dirt before reduction accomplished.

3. Dirt Removal

ne dirt should be removed in all cases. Any engine oil sepa-r of medium size is usually adequate. We have used Crane's ber 09 vertical top-inlet type (fig. 100) with excellent results. separator removes the condensation which always accumulates e pipes in some quantity in certain seasons. The Mason reduc-

ing valve, referred to above, gives excellent regulation on the reduced pressure side with fluctuations of the initial pressure ranging between 60 and 85 pounds. A large amount of work was done with this air, and no definite errors resulting from its use can, of course, be pointed out until the experiments are repeated with air of better quality. Certainly it should not be used in the most careful work.

4. Small scale methods

There are, on the market, several types of hydraulic air pumps developed particularly in connection with the compression of air for delivering liquors from barrels to the taps from which they are served. These compressors operate on the principle similar to the hydraulic ram. When connected with a large storage tank holding about thirty

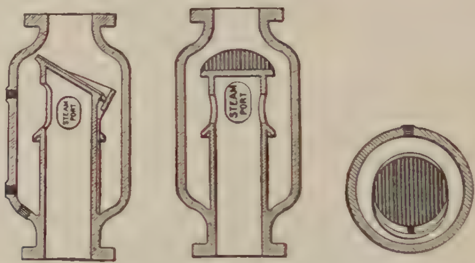


FIG. 100. Crane's no. 09 separator for recovering water from compressed air. It also removes dirt and is essential in air lines on the high pressure side of regulators (courtesy of Crane Company).

times the amount of air delivered by the pump in one minute and provided with a pop-valve to release the pressure when it becomes too high, they may be made to give fair results in ventilating a few bottles.

The Johnson Service Company's compressor has the advantage of not bringing the air into contact with the water. It is an ordinary piston compressor (figs. 101, 102, *A* and *B*). The compression stroke takes 5 seconds, and the intake stroke takes 13.5 seconds. Three of these connected so as to alternate compression strokes would give 34 liters (1.2 cubic feet) of air per minute using about 25 liters of water under ordinary conditions. One of these compressors with a storage tank at 1,000 grams per square centimeter (14 pounds) and a reducing valve delivering 15 grams per square centimeter would supply air to a few experiments.

ome pumps are open to the objection that the air comes in con-
t with the tap water directly and becomes laden with whatever
es may escape from it. The smaller type of compressor, made by
hop and Babcock, was set up and tested as shown in figure 103.
-gallon bottle was used on the suction side of the pump to take
some of the rhythmic action. A 5-gallon bottle was used on the
age side. This pump, attached to an ordinary faucet, showed
following readings on a 17-mm. gage (see p. 241) with a 6-mm.

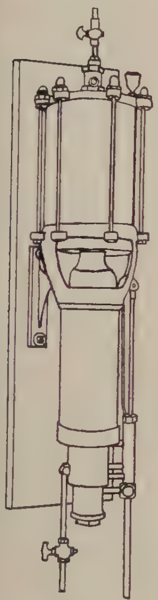


Fig. 101

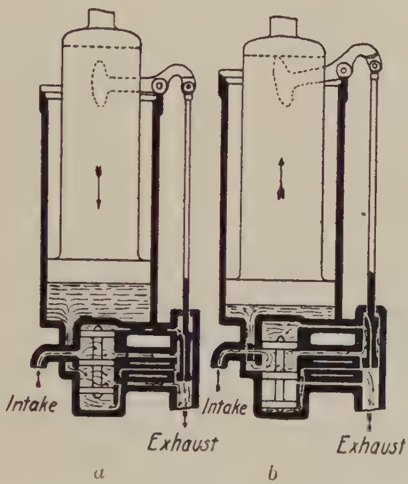


Fig. 102

g. 101. A Johnson hydraulic compressor, the upper half contains the piston.
g. 102. *a* and *b* show the lower half only with valves, etc., which raise
ower the plunger and hence work the piston in the upper half.

ture: 2.5 mm. when the pressure was lowest and 7 mm. when
pressure was highest, the medium being approximately 4.5 mm.,
h means a discharge of about 140 cc. per second (fig. 108).
intake of the pump may be used as a suction device, so that it is
ible to suck air through some bottles and deliver it to others.
n set up in the same way with a 4-mm. aperture in a gage on
uction side, the reading was from 1 to 1.3 mm. This was with
ose clamped and readings of 0.4 and 0.8 on the pressure side

with a 6 mm. aperture. Both these indicate a delivery of about 32 cc. per second at practically atmospheric pressure. Clamping down the hose did not change the fluctuations to any considerable degree.

With larger ducts small fans such as the Buffalo Forge Company blower may be used for supplying or exhausting air, but there are difficulties in regulating the flow.

5. Distribution

In all outfits where compressed air is used, the following cautions should be followed:

(1) Supply pipes must be large, about twice the size usually used by plumbers for such purposes.

(2) They should be connected with the supply tank at both ends.

(3) Gate valves of one-fourth to three-eighth inch (0.6 — 1 cm.) should be used.

(4) Hose ends on the cages and valves should not be smaller than 10.6 mm. inside diameter, that is, $\frac{1}{4}$ inch iron pipe size.

(5) Compression clamps on rubber hose should be used for regulation.

Small air supply lines or lines not connected with the supply tank at both ends show a drop in pressure with distance from the supply. The main difficulty comes in that a change in flow from one cock changes all the others.

III. SUCTION DEVICES

An ordinary hydraulic air pump, or filter pump, may be used to ventilate closed bottles. One filter pump, in good working order, will handle enough free air per minute to ventilate a number of containers (fig. 103). A suction system has the advantage that an ordinary gas meter may be inserted and the amount of gas actually pulled through the system in a given length of time can be measured, provided the vacuum developed is not so great as to injure the meter. One method of making use of a vacuum system is illustrated in figure 179, page 422, where a tank of about 500 liters capacity was used with a number of leads running to different parts of the experimental outfit. In this equipment both a small rotary suction pump consisting of an eccentric casing and the usual blades was used, though its efficiency did not greatly exceed that of the filter pump used in conjunction with it.

One difficulty with the use of suction lies in the fact that air from e immediate room is usually used, though tightly closed bottles ay be supplied with air from out of doors by a feed line.

IV. MEASUREMENT OF AIR MOVEMENT (268)

Wind velocity as commonly given in meteorological records does t represent the air movement in the usual habitat of most animals

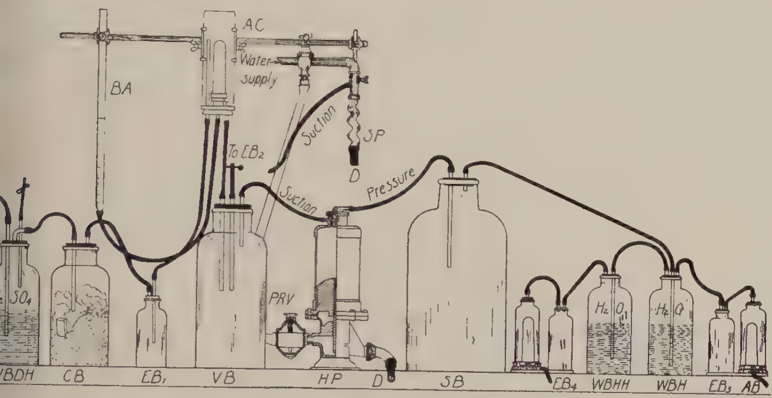


FIG. 103. Showing an arrangement of force and suction apparatus which y be attached to a water tap. *HP* is a hydraulic air suction and force pump ch exhausts air from *VB* and compresses it in *SB*, discharging water used the drain from *D*. The large storage bottles *VB* and *SB* partially comsate for the intermittent action. The combination provides for humidifica- and de-humidification and measurement of evaporation. Air taken in the pump enters at *I*, passes through sulphuric acid, in *WBDH* (water tle dehumidifier), to a bone black, charcoal and glass wool filter and then he experimental bottle *EB*. From here the air must pass over the atmom- in *AC* where the rate of evaporation will be indicated by the falling of water in the burette *BA*. The supply for EB_2 comes direct from the room. $_2$ not shown).

he air forced from the pump passes first in the storage bottle *SB*, then *VBH* (wash bottle humidifier) and to EB_3, the experimental bottle. The passes to EB_4 through a second bottle which adds more moisture. The er discharged from the pump may be used to keep one set of experiments fairly constant low temperature. The suction pump *SP* may also be used ecure ventilation in experimental cages.

n which experiments are to be made, for the anemometers are omarily set at a high elevation. If it is desired to simulate the ual atmospheric conditions of the usual habitat of an animal, the thing to do is to make observations in that habitat as a basis for nging rates of flow in the experiments. It will often be possible

to make readings simultaneously at high and low levels and thus secure a basis for comparison between the usual habitat conditions and the weather bureau records. Furthermore, the habits of the animal must be taken into account. For example, we must know whether the animal responds to air movements by taking a position either on the leeward or windward side of solid objects. If an animal living on the outside of solid objects does not respond to air move-

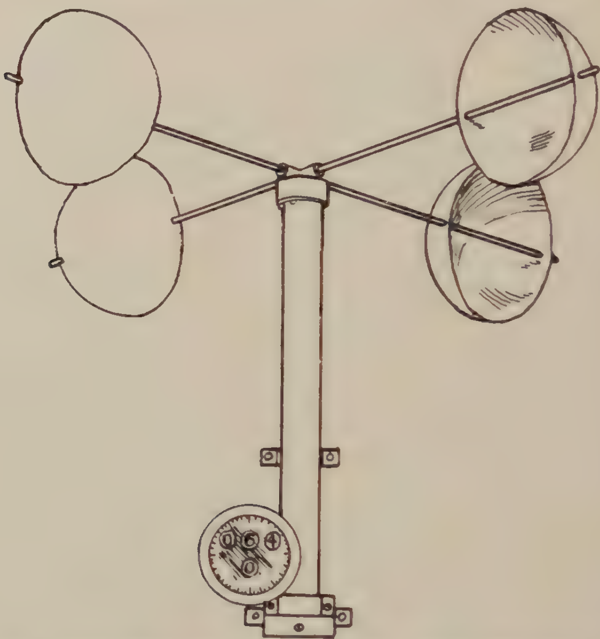


Fig. 104. A hemispherical cup anemometer which measures air from any direction, made only in large sizes.

ments, we may assume that the average air velocity over the animal's body is of the magnitude of about one-half the observed value in the habitat, for the animal presumably spends half of its time on the leeward side of the solid object. It is, therefore, seldom if ever necessary to maintain an air velocity as great as 5 meters per second in experiments, which is the average of weather bureau records for various months of the year in many localities of temperate America. It is probable that the air velocity in the habitats of most insects of

nomic importance does not exceed one-tenth the wind velocity asured by the meteorological stations.

1. Field instruments

Ieteorologists have used hemispherical cup anemometers (fig.), Biram's wind-mill type anemometers (fig. 105), pitot tubes (fig.), venturi tubes, and the Dines anemometer, which is only a moditiοn of the pitot tube. The pitot tube has two openings; one is end of the tube which faces the air current, the other a static ning facing at right angles to the direction of flow. These two

IG. 105. Shows a windmill type of anemometer which might have the fan aced by a set of cups by a skilled mechanician. Such a modified anemomevould not have the difficulty of having to face the current. Air currents quite irregular in small spaces among the vegetation where the biological stigator must make determinations (courtesy of Taylor Instrument pany).

es are connected with a U-tube gage of some form. In a Ven- tube (figure 81 shows construction) the amount of flow is indid by the difference in pressure on the side wall at the constric- as compared with the pressure where the tube is of full size. se tubes, as well as the windmill type of anemometer, must face current, and hence they are not as desirable as a small hemisrical cup anemometer for measuring air velocities among stands egetation or in the branches of trees. Unfortunately, a cup aneneter of suitable size for such investigations is not available in the estic market and must be specially constructed for such observa-

tions. Such an instrument is valuable to test the air movements in cages where eddies and back currents of various sorts may occur in the level in which the animal under observation may be living.

2. Laboratory instruments

Any device above named may be used to measure air flow in experiments, provided the containers are of such form that the device can be introduced. Biram's anemometer (fig. 105) has been used successfully in the larger cages in which a flow was maintained corresponding to that found in the animal's habitat. The flow into bottles was regulated with pinch cocks and rubber tubing and was measured daily by means of a diaphragm chamber connected with an Ellison differential draft gage as shown in figure 107. Any U-

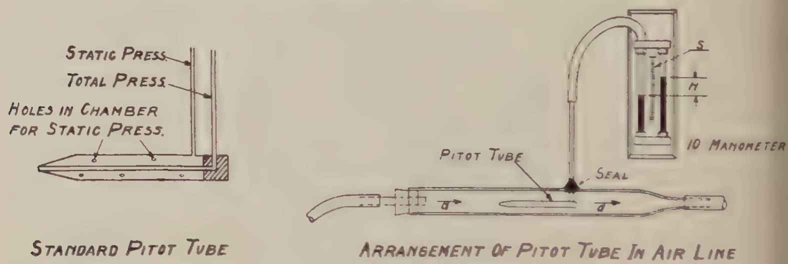
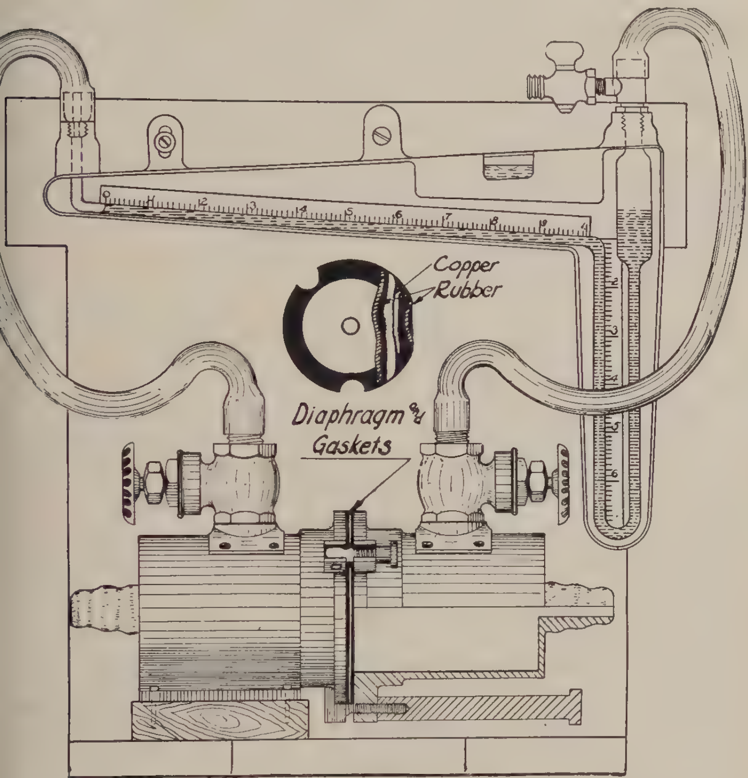


FIG. 106. A pitot tube measuring air flows especially under experimental conditions. They may be used in connection with vanes to measure air movement at different levels in a forest for example.

form gage may be used instead of the Ellison. The chamber shown in the figure has a capacity of about 1 liter and is divided into half by a thin copper plate having at its center a circular opening of known diameter. The air is introduced into the chamber at the left under pressure and is delivered at the right. The principal requirements for the successful use of this device are as follows: (1) The opening into and out of the gage chamber must be a little larger than the opening in the middle diaphragm. (2) All openings on the discharge side and all tubing used must be larger than the opening in the diaphragm. While the differential correction takes care of resistance on the discharge side, the flows are not exactly the same for like readings with and without such resistance. The accompanying technical treatment is for chambers holding about 350 cc. on each side of the diaphragm, but the tables which follow are suffi-

tly accurate for all ordinary purposes in rough experimental work. ccurate knowledge of the ventilation conditions is required a Fox- recording pressure gage may be used to record the exact condi- s continuously. The diaphragm chamber may be continuously in the air line and a continuous record made.



G. 107. A diaphragm chamber and Ellison's differential manometer grad- in inches for measuring air flows. The size of diaphragm openings and ing flows are given in figure 108. The intake and outlet tube of such a ragm chamber must be large to allow for the use of large flows through apertures. Detail of diaphragm is shown in center insert.

practice, the rubber tubes were set once a day with a suitable pinch-cock so as to give the desired flow, the gage was inserted een the air supply and the experimental container, and the read- was taken. If this reading differed from the desired flow at

which the experiment was being run, the pinch cock was adjusted to the proper point. Two readings, then, were taken each day and the mean of these was used as the mean gage reading of the experiment. To get air velocity in meters per second, the flow in cubic centimeters per second was read off from the curves in figure 108 and divided by the number of square centimeters in the area of the cage across which the air was assumed to flow, and the result was divided by 100. This method is a valid one only when used with small containers through which the air may be assumed to flow fairly uniformly.

For pressures of less than 2 pounds, ordinary illuminating gas meters may be used to measure the air flowing through experimental containers, but there is little advantage in the use of such instruments when it is merely the rate of movement that is desired.

V. CONTROL OF ATMOSPHERIC COMPOSITION

It is often desirable to control atmospheric composition especially on animals living normally or hibernating in the soil. At the Thompson Institute one line of experimentation that has been carried on is the increasing of the amount of CO_2 in the air. This was done by introducing CO_2 directly into the greenhouses above the plant tables. Apparatus for continuously recording the amount of CO_2 in the air was developed by Leeds & Northrup (746).

Hamilton (367) added CO_2 to the air used in experiments by means of the pressure reducing valve shown in the lower right-hand corner of figure 43, (Chapter III).

VI. APPENDIX

Method of determining the discharge of air through the different orifices (figs. 107 and 108) (630)

To arrive at a formula in the determination of the discharge of air through the different orifices two methods may be used:

(1) Adopting Durley's formula with other values of C, which are to be determined by experiments.

(2) Applying Bernoulli's theorem to air, i.e., the discharge = $CA\sqrt{2gh}$.

As Durley's formula is a modification of Bernoulli's theorem, the latter method is chosen. Besides, it offers a simpler means to deter-

ne the value of C for orifices of different sizes and can be easily
uced to a much simpler form for ordinary purposes.
According to Bernoulli's theorem

$$Q = CA\sqrt{2gh}$$

which

Q = volume of air discharged
C = coefficient of discharge
A = area of orifice in square centimeters
g = force of gravitation
h = differential pressure in centimeters of air

king the differential pressure in cm. of water, the formula reduces

$$Q = CA\sqrt{\frac{2gh'd',}{d}}$$

which,

h′ = the differential pressure in centimeters of water
d′ = density of water
d = density of air

ving for C gives

$$C = \frac{Q}{A}\sqrt{\frac{d}{2gh'd'}}$$

e Q, A, h', d, and d' can be obtained by experiment, and from
n, C can be calculated.

he results of a series of determinations with this apparatus are
wn in figure 108. The curves may be used in connection with
lar apparatus to determine quantity of air discharged. About
er cent deviation is to be expected with different equipment
connections.

n preparing figure 108 the quantity of air discharged through ori-
was measured by a gas meter. The differential pressure was
sured by a draft gauge for lower differential pressure, and by a
ometer for higher differential pressure. The orifices were per-
ted copper plates. The pressure of the air in the main was kept
tant at 15 pounds and was regulated by means of a rubber tube
a pinch cock.

he outlet nozzle was 8 mm. in diameter and the experiments
that for orifices equal to or larger than half the area of the

nozzle, the discharge does not materially vary with differences in the area of the orifice. For orifices of less than half of the area of the nozzle, the experiments show very good results. For differential pressure below 10 cm. of water, the coefficient of discharge C was

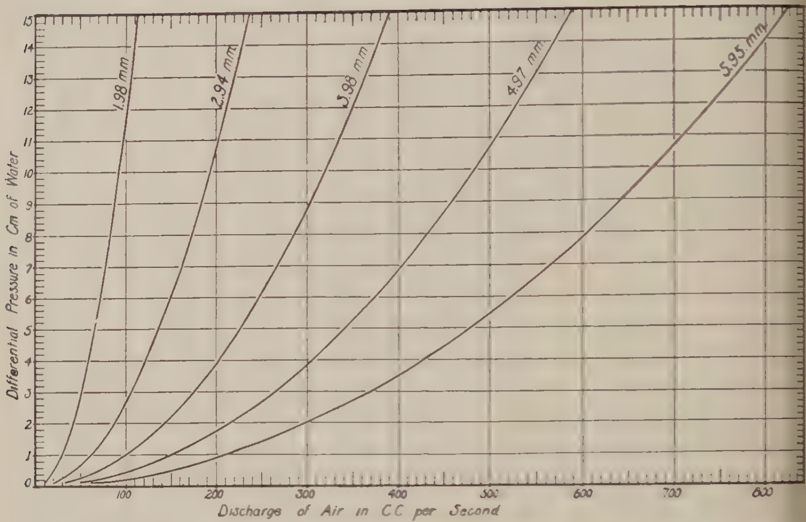


FIG. 108. Curves showing the amount of air discharged through various apertures in the chamber shown in figure 107. The discharge is in cubic centimeters per second and the pressures in centimeters of water.

TABLE 20

Diameter of orifice and corresponding value of C

NUMBER	DIAMETER		A	A	AVERAGE C
	inches	*mm.*	*sq. mm.*	*sq. cm.*	
1	0.078	1.98	3.08	0.0308	0.739
2	0.116	2.94	6.79	0.0679	0.700
3	0.157	3.98	12.46	0.1246	0.633
4	0.196	4.97	19.40	0.1940	0.613
5	0.234	5.95	27.80	0.2780	0.600

nearly constant, but at higher pressures the value of C changed abruptly.

Table 20 shows the diameters for the different orifices used in the experiment and the corresponding value of C.

ues shown graphically in figure 108 were calculated by the for-

$$Q = CA\sqrt{\frac{2gRd'}{d}}$$

ich

= cubic centimeters of air per second at 76 cm. and 23°C.
= differential pressure in cm. of water
= coefficient of discharge
= density of water at 23°C.
= density of air at 23°C., 76 cm.
= area of aperture

CHAPTER X

The Control and Measurement of Moisture

I. INTRODUCTION

Moisture reaches ordinary terrestrial animals (1) as rain or mist which comes into contact with their bodies temporarily, or (2) as temporary standing water collecting in the cavities in which they live, or (3) as atmospheric humidity. All three are of much importance and must be fully considered in experimental work. Failure to imitate these conditions in experiments has been fully as important in preventing progress as the misconception regarding temperature relation. Such papers as those by Greeley (345), Fuller (318) and Walker (937) illustrate the supposed conditions and general effects of moisture conditions. Headlee (381) and Hefley (382) have made important experimental studies.

II. CONTROL OF MOISTURE

1. Rain

Experimental reproduction of rain has probably seldom been accomplished. In a few cases it has been applied to cultures of insects on their food plants by W. L. Tower. Doubly distilled or otherwise pure (salt-free) water should be used. Where distilled water is used with a sprayhead some method of securing pressure must be devised. Sprayheads are not ordinarily desirable because they do not spread the water evenly at close range. In general, the ordinary sprinkling rose will probably serve better. In cages with plants on which insects are grown, such imitation of rain is very desirable in connection with experiments designed to simulate all conditions of water. A daily exposure to rain may be desirable for certain insects, in imitation of certain seasons and climates. This may be accomplished by means of a program clock which empties a definite quantity of water through a rose and on the plant daily. If the quantity of water is large, provision will have to be made for surface and bottom drainage of the soil by some means which will not permit the escape of the insects.

2. Soaking

Quiescent stages of all kinds may be soaked, i.e., submerged in ter for periods of two to twenty-four hours more or less. Townid (903) found that frequent soakings gave results in breaking up rmancy in codling moth larvae. Infrequent soakings had failed do so in most cases in experiments by the author evidently because ey were not sufficiently frequent. If soakings are to be carried on, preliminary series of experiments should cover various periods of omergence in order to ascertain the time to death.

3. Air humidity

Air humidity is one of the most difficult factors to control because fluctuates so greatly with temperature changes. In treating air oplies for experimental work, two processes are commonly involved, midification and dehumidification (451).

Devices for humidifying and dehumidifying entire rooms or small ambers have been installed in connection with various commercial erprises and, in a few cases, for scientific experimentation. For periments with large animals, such as sheep, poultry, and cattle, se commercial methods are sufficiently well adapted to the purpose enable those desiring to install such equipment to leave the matter he hands of engineers who make such work their principal business. has already been noted, however, that the methods commonly ployed in this kind of work are not well adapted to economical erimentation on small animals, such as rats, mice and insects, ere it is desirable to run a considerable number of different eximents in small cages or containers at different temperatures, nidities, pressures, and air velocities. It is, accordingly, imtant to consider methods of humidifying and dehumidifying small ntities of air.

4. Humidification

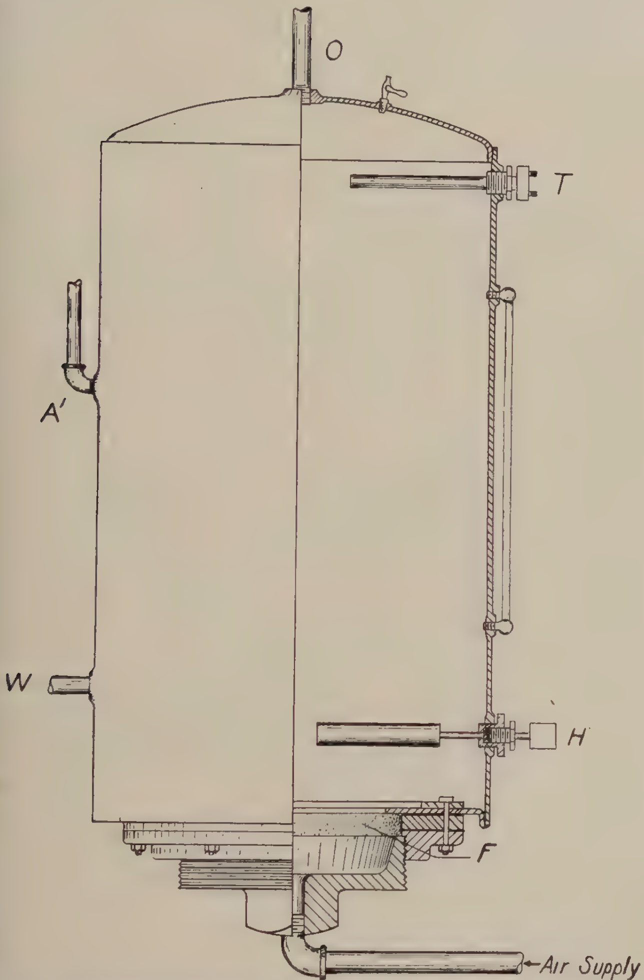
. *Correct method.* The correct principle for the control of humid- is based on dew-point temperature for the desired humidity, t is, the temperature of saturation and condensation of water or. The air is saturated with water vapor at the dew-point temature of the desired temperature and humidity. For example,)°C. and relative humidity 70 per cent are desired, air must be urated at 15°C. and warmed to 20°C. without contact with water.

If a humidity of 20 per cent is desired the air must be saturated at approximately −0.5°C. and warmed without contact with water. Apparatus which uses this method gives a constant humidity free from oscillations. Humidity is regulated by increasing or decreasing the temperature at which the air is saturated with moisture. Conditions for the saturation of the air must be such that it can take place with a fair degree of certainty. This usually means atomizing the water at the dew-point temperature into the air to be treated. All other methods of saturating air are likely to be less reliable and less effective. Potter (683) emphasizes the method of using water to control humidity on account of the fact that it removes much of the dust and dirt and partially sterilizes the air used.

b. Wash bottles. Humidification in simple experiments in bottles, for example, may be accomplished by means of an ordinary wash bottle such as is used in chemical laboratories. The distance of the inlet tube above or below (just above the surface is most effective) the surface may be used to regulate humidity. The water level must be nearly constant. This can be accomplished by adding a small amount from a separatory funnel inserted in the cork from time to time, when the experiments are being observed. Humidity can be further regulated by controlling temperature surrounding wash bottles (figure 103, Chapter IX).

c. Tanks. The type of device best adapted to the humidification of larger quantities of air is a tank built on the principle of the wash bottle and equipped with a brine coil or an electric heater, as shown in figure 109, to maintain the water at a constant temperature. The thermostat which turns on the current for the electric heater or the brine for the coil should be located in the air chamber, not in the water. The water supply is maintained at a constant level by means of a supply tank containing distilled, boiled, or thoroughly aerated water. The tank should remain constantly about half full of water so that a considerable body of air is in the tank for some time in contact with the water. The air should enter over a large area and through very small openings, so that it passes through the water in a finely divided state. For this purpose a large filtros plate can be inserted in the center of the bottom of the tank as shown in figure 109. Filtros is an artificial porous stone with practically uniform structure analogous to a mass of capillary tubes which take a tortuous course through the material. It is made in four grades, "coarse,"

edium," "fine," and "dense." The selection of the grade for a
idifying tank depends upon the air pressure to be used and the
unt of dirt in the air.



G. 109. A warm water humidifier with filtros plate (F) for admitting air;
r (H), thermostat (T) showing connection with a small tank A′ and W
tting water when the level falls (see fig. 176).

Spray chamber (152). The usual method of humidifying air
entilation in buildings consists in spraying finely divided water

into the air, the water being maintained at a temperature necessary to give the desired humidity. Water from the city supply is commonly used. Its temperature is commonly lower than that of the rooms into which the air is to be carried, so that the air is at the same time both cooled and moistened so as to approach saturation at the temperature of the water. In such cases the water is often

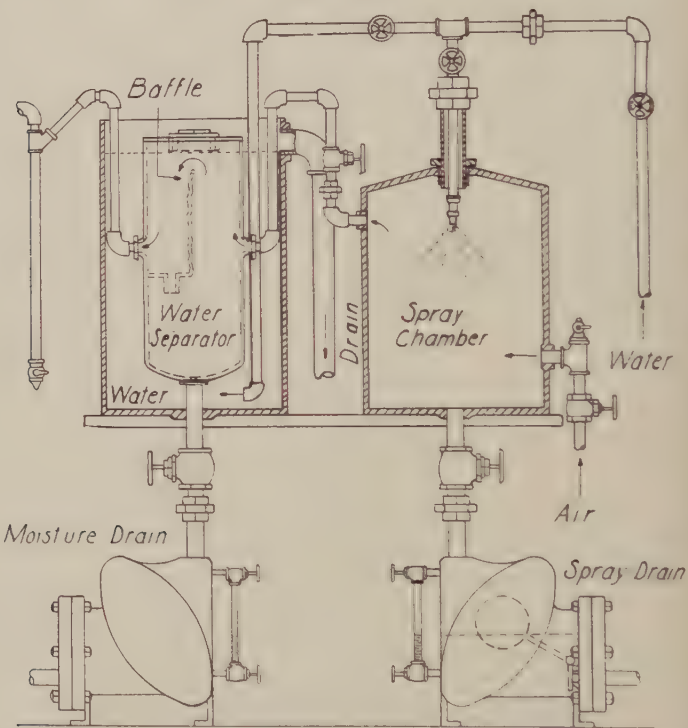


FIG. 110. A small spray humidifier with separator to remove water and ball float cocks to drain both chambers.

allowed to flow away into the sewer. Where temperatures other than that of the city water are required, it is necessary to heat or cool the water to the desired temperature, which is an expensive process unless the water is recirculated. Recirculation involves a pump, storage tank, and power as well as some heating or cooling coils to maintain the desired temperature. Where the tap water contains no injurious gases or other undesirable substances, a device such as is

n in figure 110 can be used. The air enters a small 40-liter
y chamber supplied with tap water and passes from this to a
e chamber designed on the lines of the Crane ammonia oil separa-
nd surrounded by running tap water. Both the baffle and spray
ıber are drained by ball float steam traps. When used by the
er, this device delivered 50 liters per minute at about 90 per cent
ration at the temperature of the tap water. This type of device,
ever, is limited in its application and open to criticism on ac-
t of gases likely to be added to the water.

Dipping asbestos sheets or fabric sheets (706). Sheets of asbestos
r or suitable fabric dipping in an open tank may be used to sup-
noisture to passing air. The area of sheet exposed above the
r and the character, i.e., whether a salt solution or pure water,
depth of the water determine the humidity. Where there is
much air movement, such a method may be put under humido-
c control by raising or lowering the sheets or the water level
matically.

A constant humidity in still air (611). In closed vessels the de-
constant humidity may be maintained with salt solutions, as
n in table 21, or with sulfuric acid solutions, as shown in table 22.
humidities given in table 21 do not hold exactly for temperatures
than those stated. In most of the cases where several tempera-
are given in the International Critical Tables (611) the humid-
s lower at the higher temperature, but within life ranges the
rence in degrees is about twice the difference in percentage of
dity. The humidities resulting from the use of sulfuric acid
ıot materially changed by difference in temperature within life
es.

5. *Dehumidification*

Acid dehumidifiers. Dehumidification may also be accom-
ed by means of sulfuric acid. The vapor tension of sulfuric
s so low that it has little tendency to pass beyond the container
ich the air comes into contact with the acid. Usually the best
s are obtained by having the intake tube of the wash-bottle
above the surface of the acid rather than below the surface.
nd the acid-containing bottle there should always be a bottle
ed with glass wool and beyond this a bottle containing charcoal.
r these conditions no acid vapor appears to pass into the ex-

TABLE 21 (611)

Constant humidity maintained with salt solutions

SALT	TEMPERATURE	HUMIDITY
	°C.	per cent
H_3PO_4	24.5	9.0
$KC_2H_3O_2$	20.0	20.0
CRO_3	20.0	35.0
$CaCl_26H_2O$	5.0	39.8
$CaCl_26H_2O$	20.0	32.3
$CaNO_24H_2O$	18.5	56.0
$CaNO_24H_2O$	24.5	51.0
NH_4Cl	20.0	79.0
KBr	20.0	84.0
$CaSO_45H_2O$	20.0	98.0

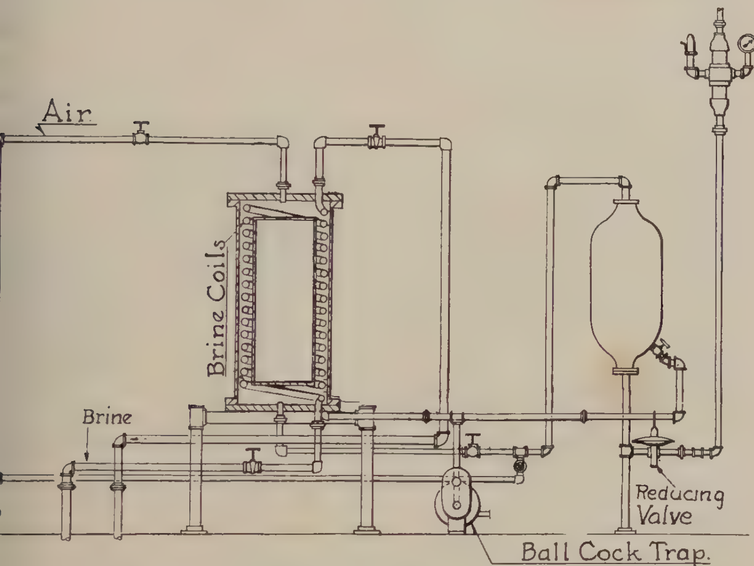
TABLE 22

Approximate relative humidity, vapor pressure and saturation deficit at 20° and 30°C. for dilute sulphuric acid of various specific gravities (861)

SPECIFIC GRAVITY	PERCENTAGE H_2SO_4 IN THE SOLUTION	APPROXIMATE RELATIVE HUMIDITY	VAPOR PRESSURE AT 20°C.	SATURATION DEFICIT AT 20°C.	VAPOR PRESSURE AT 30°C.	SATURATION DEFICIT AT 30°C.
		per cent	mm. of mercury		mm. of mercury	
1.00	Water	100.0	17.39	0.0	31.55	0.0
1.05	7.37	97.5	17.0	0.4	30.7	0.8
1.09	12.99	94.8	16.5	0.9	29.9	1.6
1.12	17.01	92.3	16.1	1.3	29.1	2.4
1.14	19.61	89.9	15.6	1.8	28.3	3.2
1.18	24.76	84.0	14.6	2.8	26.5	5.0
1.20	27.32	80.5	14.0	3.4	25.4	6.1
1.23	31.11	74.6	13.0	4.4	23.5	8.0
1.25	33.43	70.4	12.2	5.2	22.2	9.3
1.27	35.71	65.5	11.4	6.0	20.6	10.9
1.29	38.03	60.7	10.6	6.8	19.1	12.4
1.30	39.19	58.3	10.1	7.3	18.4	13.1
1.344	44.0	49.0	8.5	8.9	15.5	16.0
1.361	46.0	45.0	7.7	9.7	14.5	17.0
1.438	54.0	29.5	5.0	12.4	9.5	22.0
1.479	58.0	21.5	3.5	13.9	7.2	24.3
1.524	62.0	15.5	2.6	14.8	5.0	26.5
1.569	66.0	10.5	1.8	15.6	3.5	28.0
1.639	72.0	6.0	1.0	16.4	2.0	29.5
1.710	78.0	3.0	0.4	17.0	1.1	30.4

imental chamber. However, it is obvious that the air is slightly dified in passing over the acid because organic matter in it is ely to be converted into a minute trace of gas, e.g., H_2S. While s method is an undesirable one, it is one which the investigator hardly hope to discard, as it extends the number of experiments ich may be run in small containers.

. *Low temperature dehumidifiers* (152, 543). For large chambers air is cooled to a low temperature in contact with water, which



IG. 111. A spiral coil dehumidifier complete with brine supply, Crane rator and pressure reducing valve. The condensation accumulating in brine coil chamber leaves through the ball float trap.

ngs it to a saturation point at that temperature, and then warmed in, so that its relative humidity is lowered to the desired point. e spray method is commonly used and the water is recirculated r refrigeration coils for cooling.

Dehumidification is most readily accomplished by passing the air r brine coils from a refrigerating plant and by drawing the water ondensation through a ball float steam trap. Figure 111 shows a umidification device used at the University of Illinois in which a al pipe coil is enclosed in a cylinder. The dehumidification takes

place at high pressure, and the pressure reduction is accomplished afterwards. The brine coil, a spiral made from 1-inch iron pipe, is enclosed in a casing made from spiral riveted pressure pipe, diameter 37 cm., 75 cm. long, provided with end flanges. The brine coil fits tightly against the inner wall of the pipe, and the space in the center of the coil is occupied by a galvanized iron cylinder with closed ends. There is a small hole in the cylinder to maintain the air pressure the same inside and out, thus preventing its collapse. The ends of the large pipe were covered with circular iron plates bolted to the flanges.

Double pipe dehumidifiers, from simple double pipe fittings, have been found to be very effective. In all these devices the excess moisture is withdrawn through ball float cock steam traps. Duplicate coolers are important where continuous operation is anticipated. This method is open to the objection that a definite humidity can not be maintained. The amount of ice on the coils, the temperature of the brine, the speed of its circulation, and various other factors tend to render the results of such dehumidification variable, but it may be utilized by controlling the brine flow. It must, therefore, be used with regulatory devices and must be built in duplicate to allow thawing. For work where constant low humidities are desired, a plan essentially identical to that shown in figure 109, except that a brine coil takes the place of the electric heater, may be employed, if working temperatures are relatively high. This method is limited to temperatures above freezing.

6. *Humidity regulation*

This may be accomplished through the regulation of the saturation temperatures when water is used, as has been suggested in connection with humidification.

A principle sometimes employed for controlling humidity consists in maintaining a constant dry bulb temperature (temperature control) and at the same time a constant wet bulb temperature. If both are maintained, a constant humidity results. The temperature of the chamber is maintained by a dry thermostat while the humidity is controlled by the thermostat surrounded with cloth saturated with water. The difficulties arising with this system are that the water supply for the wick must be maintained, air movement must be maintained to keep evaporation at a maximum, and the wick must

be kept clean. The covering of the sensitive part of the bulb thermostat should be so constructed as to make possible its rotation so that a sheet wicking can be used, and a new portion turned on each day. The difficulties connected with maintaining the wet bulb temperatures make it a poor method to use.

A method which has been used quite extensively in the work at the University of Illinois consists in mixing wet and dry air in a tank under humidostatic control. The Johnson direct and reverse action valves are used on the wet and dry air supply. The Johnson insertion type humidostat with a leak port outside is used for control-

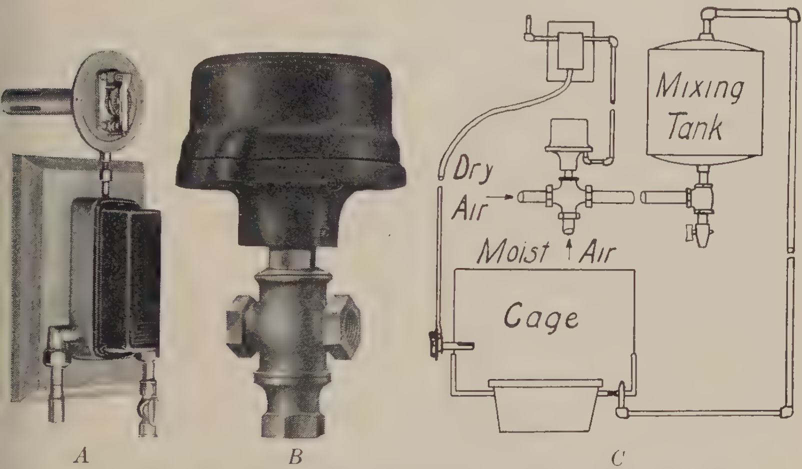


FIG. 112. Insertion humidostat intermediate type (*A*) and three way valve (*B*) (courtesy of Johnson Service Company). The arrangement of parts connected with a cage is shown in *C*.

ling the humidity. This system gave unsatisfactory results. The apparatus was so arranged that the action of the humidostat, when the air in the mixing tank became too moist, turned on the dry air for a short time until the reversed action of the humidostat turned on the wet air again. The difficulty of this system arose from the use of positive valves. With intermediate valves, it gives fairly satisfactory regulation when the difference in the humidity of the two airs mixed is not too great. It should not be more than 15 per cent.

The Carrier vapor pressure hydrostat (no longer manufactured) was a unique instrument based on the fact that the ratio of sulfur

dioxide pressures corresponding to wet and dry bulb temperatures is substantially constant at any per cent of humidity for any range of dry bulb temperatures between 16° and 38°C. This made it possible to oppose the opposite pressures at any desired ratio corresponding to any desired humidity controlled throughout any range of dry bulb temperatures. This instrument is an important one and its principle should be known to biologists.

The mechanism of the Leeds & Northrup recorder could also be used to control humidity (fig. 96 and p. 225).

III. MEASUREMENT OF MOISTURE (150, 402, 579)

In soil and materials surrounding animals, moisture is commonly determined by weighing, desiccating at 105°C., and determining per cent of water.

Air moisture is determined by the following methods: (1) absorption with sulfuric acid, (2) determination of the temperature of dew-point, which is just in excess of saturation, by cooling the air and noting the temperature at which moisture is precipitated, (3) determination of the difference in temperature of a dry thermometer and a wet bulb thermometer.

Humidity is also determined by hairs or other hygroscopic substances standardized from time to time by one of the methods enumerated.

1. Psychrometers

For determinations in the open air, the sling psychrometer seems most practical, and there are various methods of securing high air velocity.

Enclosed wet and dry bulb thermometers as shown in figure 113 are useful in experiments where air under pressure is used to ventilate containers.

2. Dew-point apparatus (579)

The apparatus shown in figure 114 is a modified form of Regnault's apparatus, and serves to determine directly the temperature of the dew-point. It consists essentally of a thin polished silver tube, *a*, cemented upon the lower end of a longer glass tube, as shown. The stopper closing the upper end of this tube is fitted with two lateral tubes of hard rubber, *b* and *c*, and carries a delicate thermometer, the

bulb of which is placed near the center of the silver tube. The tube b extends to the bottom of the silver tube; c projects but a short distance through the cork. A rubber aspirating apparatus, as shown, is connected with the tube b, and a long tube joined to c serves to carry off the fumes generated in the apparatus. The glass tube is held in a clamp faced with cork, which largely intercepts the transfer of heat.

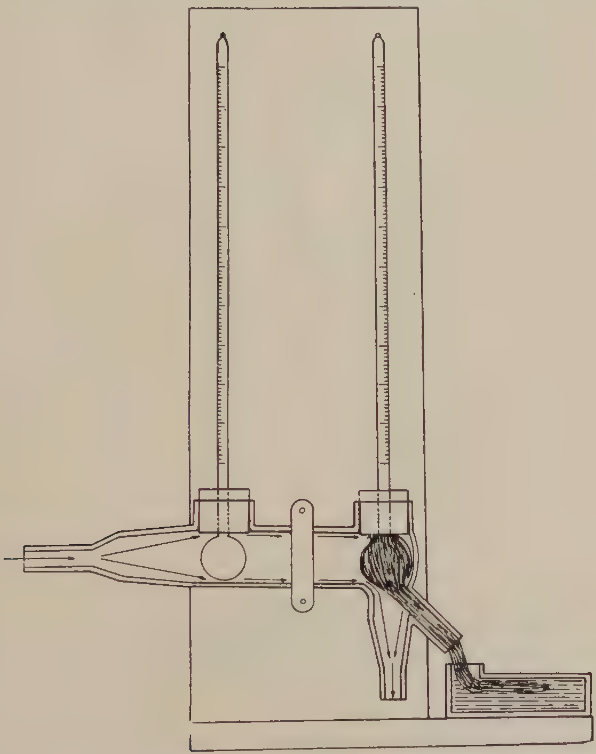


FIG. 113. Wet and dry bulb thermometers for measuring air discharge from pipes.

Observations are made by filling the silver cup with sulfuric ether, or similar volatile liquid, which is caused to evaporate and cool the silver cup in the desired manner by manipulating the aspiration bulb. At the proper point of cooling, a deposit of dew is seen to form on the polished silver surface. The object is to ascertain accurately the temperature at which the dew will just deposit. For this purpose

it is necessary that the temperature be lowered very slowly at the critical point, also that there be plenty of liquid in the cup and that it be agitated sufficiently to have a uniform temperature throughout. Finally, the surface of the silver must be perfectly clean and in a favorable light, so that the faintest deposition of dew is at once visible. The temperature shown by the thermometer at this moment may be regarded as the temperature of the dew-point.

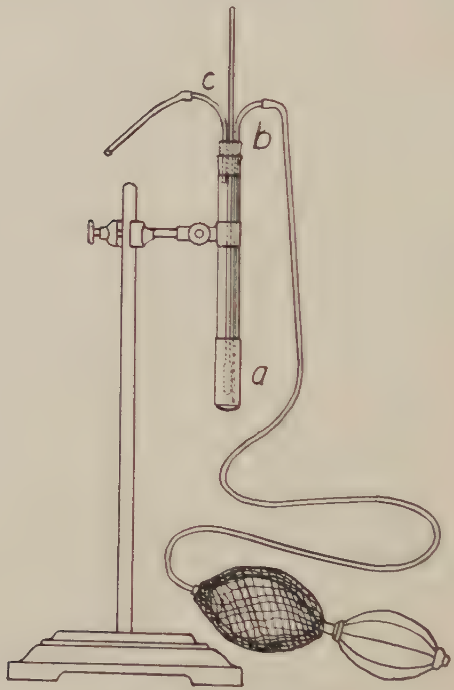


Fig. 114. Dewpoint apparatus with mercury thermometer

In order that the presence of the observer shall not affect the moisture contents of the air in the vicinity of the cup during an observation, it is necessary that in breathing he exhale through a suitable tube which will conduct the moist air from his lungs to a sufficient distance. It is further advisable that a very gentle motion be given to the air near the cup by use of an ordinary fan. For the greatest accuracy, the cup should be allowed to warm up and the deposition of dew formed several times in succession, a reading of the temperature being made at each deposition.

Holtzman (407) has described two thermocouple dew-point instruments as shown in figure 115, *A* and *B*; the apparatus appears suitable for enclosure of the rod in a clear glass tube into which very small amounts of air might be drawn from an enclosed space and the dew-point determined.

Mr. D. C. Lindsay has an apparatus in preparation in which the silver area is a small point. This apparatus might be inserted into small spaces. Such instruments must be carefully made so that the temperature read on the thermometer is the same as the temperature of the bright metal on which the moisture is deposited.

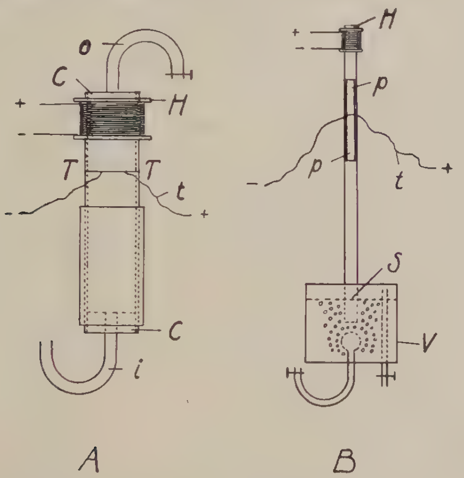


FIG. 115. Thermocouple dewpoint apparatus

A. For use in small enclosures. The copper tube *C* is supplied with an inlet (*i*) and an outlet (*o*) so that a cold fluid may be run in. The small coil (*h*) is a heater which warms the upper end of the tube, a thermocouple is soldered to a scratch on the tube. The temperature is read when the mist on the tube reaches (*T*).

B. The principle is the same as in *A* but a silver (polished at *p*) rod is cooled by vaporizing ether.

The values of relative humidity, and the temperature of dew-points given in the United States Department of Agriculture, Psychrometric Tables, have been computed by means of the following formula, deduced by Professor Ferrel,

$$e = e' - 0\,000367\,P\,(t - t')\left(1 + \frac{t' - 32}{1571}\right)$$

in which t and t' are the temperatures of the dry and wet bulb ther-

mometers, P is the barometric pressure of the air in inches, all corrections having been applied, and e' is the maximum or saturation pressure of aqueous vapor at the temperature t' of the wet bulb.

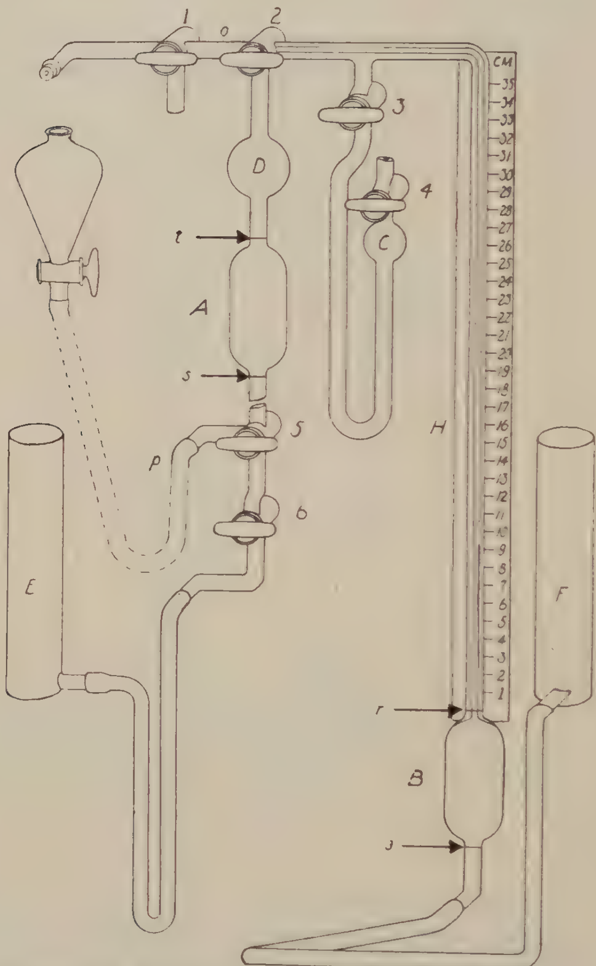


FIG. 116. Chemical hygrometer; modified Rideal and Hanna (739) apparatus.

The solution of the equation gives e, the pressure of the aqueous vapor corresponding to the observed temperatures t and t'.

3. *Acid Hygrometer*

The chemical hygrometer, a modified Rideal apparatus (739), (fig. 116), consists of a calibrated stem *H* of known uniform diameter and of two bulbs, *A* and *B*, of the same capacity between the levels indicated by the arrows. The bulbs are connected at their lower ends to two movable mercury reservoirs packed in glass wool in metal holders (*E* and *F*), suspended on ratchets. Above the mercury in the bulb *A* are a few cubic centimeter of strong sulfuric acid, occupying the bulb *D* when *A* is full of mercury. The stem *H* of the bulb *B* carries merely a millimeter scale; if desired, it may be calibrated in per cent.

TABLE 23

Showing specifications for H_2SO_4 hygrometer

CAPACITY OF BULB	DIAMETER OF TUBE	LENGTH OF TUBE FOR DIFFERENT TEMPERATURES AND SATURATION		
		30°C.	38°C.	45°C.
cc.	*mm.*	*cm.*	*cm.*	*cm.*
50.0	3.0	30.0	46.9	
35.0	3.0	21.1	32.8	47.5
20.0	3.0	12.1	18.7	27.1
35.0	2.0	47.3		
20.0	2.0	27.0	42.2	
10.0	2.0	13.5	21.1	30.5
5.0	1.0	27.1	42.3	
2.0	0.5	43.4		
1.0	0.5	21.7	33.9	48.8
0.5	0.4	16.9	26.4	38.1
0.5	0.3	30.1	47.1	

The principle of operation depends upon the ratio of the capacity of *H* per unit of length to the capacity of *B*. This makes possible the determination of the ratio between the shrinkage due to absorption of the water vapor and the original volume. The hygrometer may be made in any size. The bulbs and the diameter of *H* may both be very small.

In drawing up specifications for the diameter it is necessary to consider the maximum shrinkage, the amount of air that may be obtained, and the length of tube comparable with handling. In field equipment the tube must be short.

With the principle of measurement made clear, the essentials of construction relative to manipulation and adjustment to atmospheric pressures must be considered. The upper end of the calibrated tube and the stem of the sulfuric acid bulb are connected by means of a three-way cock, *2*, and a horizontal capillary tube, which is also connected to an aniline U-tube, fitted with a bulb *C* to compensate for any small changes in temperature or pressure taking place during the experiment.

In Rideal's apparatus there was but one three-way cock in the horizontal capillary. The tube stood open to the air at *O*. The three-way cock *1*, is necessary in taking samples from soil or small enclosures. In so doing, a capillary rubber tube bearing a hollow needle at the end is inserted into the soil at the desired depth. Cocks *1* and *2* would be turned ⊤ and the mercury reservoir lowered so as to fill the tube with air from the source desired. After the rubber tube, etc., outside of *1* is filled, cock *1* is turned into the position ⊢ and the excess air forced out. This operation may be repeated until the error due to air in the capillary rubber tube is reduced to a negligible amount.

Cocks *5* and *6* were also added to Rideal's original apparatus to facilitate changes in the sulfuric acid. To put acid in the reservoir, *E* is lowered with *5* and *6* open downward until the mercury stands just below *5*. Cock *6* is then closed and *5* turned ⊥. Sulfuric acid may then be changed. Cock *6* should be closed whenever the apparatus is left, as an inadvertent lowering of bulb brings the sulfuric acid in contact with the rubber, which it destroys, and after a time releases the acid mercury, with considerable damage resulting.

The horizontal capillary tube above *3* is also connected to an aniline U-tube, fitted with a bulb *C* to compensate for any small changes in temperature or pressure taking place during the experiment. This U-tube contains a small amount of mercury or colored manometer oil which stands at the same level in the two arms when the pressure is equalized.

The reservoir *E* is raised until the bulb *A* is full of mercury, i.e., exactly to the upper mark, and the sulfuric acid above it all but

fills the bulb D. A sample of fresh air is drawn into B through *1* and *2* ($\perp$) by lowering F. The compensator and gauge cocks *3* and *4* are opened, thus insuring that the sample in B is at the same temperature and pressure as the surrounding air. The cocks *3* and *4* are then closed and the bulbs B and A connected by turning cock *2*. The air in B is transferred to the sulfuric acid bulb by raising the reservoir F and lowering E. When the mercury in B rises to the mark r and the level in A has reached s, the cock *3* is opened connecting the air inside the bulbs D and A to the gauge. Since the volume of mercury entering B is exactly equal to the volume leaving A, if the air were perfectly dry, no change in pressure would be observed, but with ordinary moist air a contraction is noticed and the mercury is no longer level in the two arms of the U-tube. It is then necessary to raise the level of mercury in the calibrated stem H at the same time maintaining the mercury level at s in the other arm until the gauge comes into equilibrium. The actual quantity of moisture removed from the air can then be directly read off on the stems H, by reading the rise of the mercury.

The tube H may be calibrated in per cent saturation or vapor pressure in millimeters of mercury. If per cent of saturation is used, corrections for temperature and pressure must be made. An accurate thermometer and a barometer must be available. Acid must not be allowed to rise beyond bulb D and get into the capillary tubes.

The objection to apparatus which necessitates the return of the air to another chamber after drying is that the dried air takes up water, owing to the hygroscopic nature of the glass. It is often necessary to pass the air over eight or ten times before being thoroughly dried.

IV. HUMIDITY RECORDING (70)

Humidity recording devices usually consist of a group of human hairs or other hygroscopic fibers connected with a pen which is in contact with a rotating drum. This type of instrument is the only type that is commonly on the market and suitable for recording humidity directly in per cent of saturation. (Other common types of humidity recorders consist of wet and dry bulb thermometers which record on the same sheet, showing difference in wet and dry bulb readings at various hours. From this, however, one must derive the relative humidity from tables and draw the curve on the sheet.)

This is probably the most accurate, simple method, at present, available. The hygroscopic hairs do not retain standardization and should be standardized with a sling psychrometer every week. The instruments are practically much more accurate than commonly supposed because a difference of one per cent of humidity has less than a third as much effect on rate of development as a difference of 1°C. Most of these devices unfortunately do not lend themselves to the development of the insertion type of sensitive parts. All are large, awkward devices. A plan has been proposed by a member of the firm of Julien Friez & Sons to insert the sensitive part inside a cage. The frame holding the hairs can be fixed on the inside of the cage and the case of the instrument placed in a solid position outside the cage. An aluminum wire can then be used to connect the hairs with the hook which usually attaches to them. The hole through which the wire passes should be large and closed with a bolting cloth cone which is attached to the wire.

The Leeds & Northrup humidity recorder involves the principle used in all recorders manufactured by this firm. The following description is taken from Behr (70):

Recorder mechanism. A mechanism is described capable of automatically balancing any network of impedances where the balance point is attained by the motion of one or more sliders along slide wires, and where the balance point is determined by the absence of current in the recorder galvanometer.

Relative humidity curves. From the formula for relative humidity in terms of the wet and dry bulb temperatures, it is shown that for constant humidity the relation between wet and dry bulb temperatures is very nearly a linear one, and that the value of the humidity is uniquely defined by the ratio (wet bulb temperature—A)/(dry bulb temperature—B) where B is a constant and A is a function of the relative humidity but changes only slightly with it.

Recorder circuit. By using a nickel resistance thermometer in a net-work which is essentially a split circuit potentiometer, it is possible to secure a potential difference across the ends of a slide wire which is directly proportional to (dry bulb temperature—B). In another very similar circuit a potential difference is gotten which is proportional to (wet bulb temperature—A). This latter potential difference is automatically balanced against a portion of the former by the recorder mechanism mentioned above, and the position of balance is indicative of the ratio (wet bulb temperature—A)/(dry bulb temperature—B) so that the instrument reads directly in relative humidity.

The results of a check on the finished instrument are given from which it appears that the approximations made in the design and any inaccuracies introduced in the actual construction are of no greater magnitude than the uncertainties in the humidity formula itself.

Maintenance of wet bulb. Two forms of wet bulb are described which are capable of continuous operation. In one the customary wick is replaced by a spray, and in the other a long wick is provided so that a clean portion can be substituted for the soiled part merely by turning a roller to wind the wick from one holder on to another.

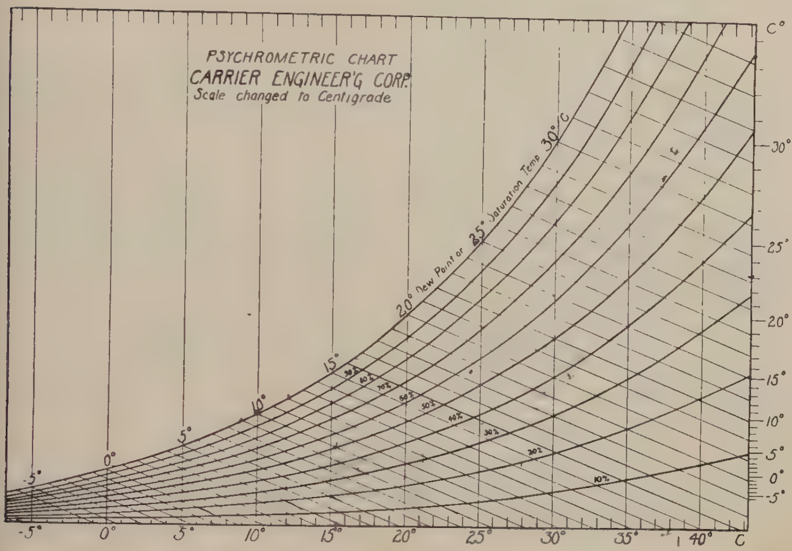


FIG. 117. Carrier Engineering Corporation's Psychrometric chart (in part) converted into Centigrade. For example; given a dry bulb temperature of 30° and a wet bulb temperature of 22°. Locate the point of intersection of the vertical line representing dry bulb 30° and the oblique line representing 22° wet. The point of intersection of these two lines shows the relative humidity to be 50 per cent; following to the right parallel to the base a dewpoint of 19.7 is indicated. Further a relative humidity of 30 per cent with dry bulb 20° would be 20 per cent if warmed to 27.5° as is sometimes necessary.

If the dry bulb temperature is constant and a constant humidity is required, some of the circular wet and dry bulb recorders can as well be used at less expense.

CHAPTER XI

Temperature and Humidity in Combination

I. INTRODUCTION

In nature, temperature and humidity vary together and roughly reciprocally. If these two factors can be evaluated in respect to their combined effects upon animals, the evaluation of other factors such as light intensity, rainfall, etc., should be greatly facilitated. Probably for most organisms in north temperate regions, development is increased in rate by an increase in humidity, up to a fairly high optimum, but data are available for only a few. The relation between the rate of development or other life phenomena and the *combination* of temperature and humidity has been worked out but slowly and incompletely. Some of the first suggestions were from Abbe (1) and Griffith Taylor ((508, 881). Pierce (676) next showed this kind of relation, evidently very schematically, for the boll weevil. It is the purpose of this chapter to indicate the methods for determining and representing such a relation.

II. HUMAN DEATH RATE (419)

The first important interpretation of biological relations in which definite phenomena were drawn to scale was Huntington's study of death rates in relation to mean daily temperature and humidity (419). Figures 118 and 119 are taken from his work, the one showing actual percentages above and below the normal death rate at different temperature-humidity combinations, and the other showing smoothed curves at 5-unit intervals for the same data. For purposes of illustration we have combined death rate data in three of Huntington's equal death rate charts to make the survival curves shown in figure 120 and the survival chart shown in figure 121. These survival curves correspond to the velocity curves which may be drawn for temperature as shown in Chapter VII, though here and in connection with such charts generally, there is a curve for each humidity. The generalized curves of relative survival shown in figure 120 have been constructed by use of Huntington's data for

southern France, northern Italy, and southeastern United States (the last being included to represent warm moist conditions). In his original figures, the data were expressed in per cent above and below the normal death rate, and the difference between the highest rate (under most adverse conditions) and the lowest rate (under

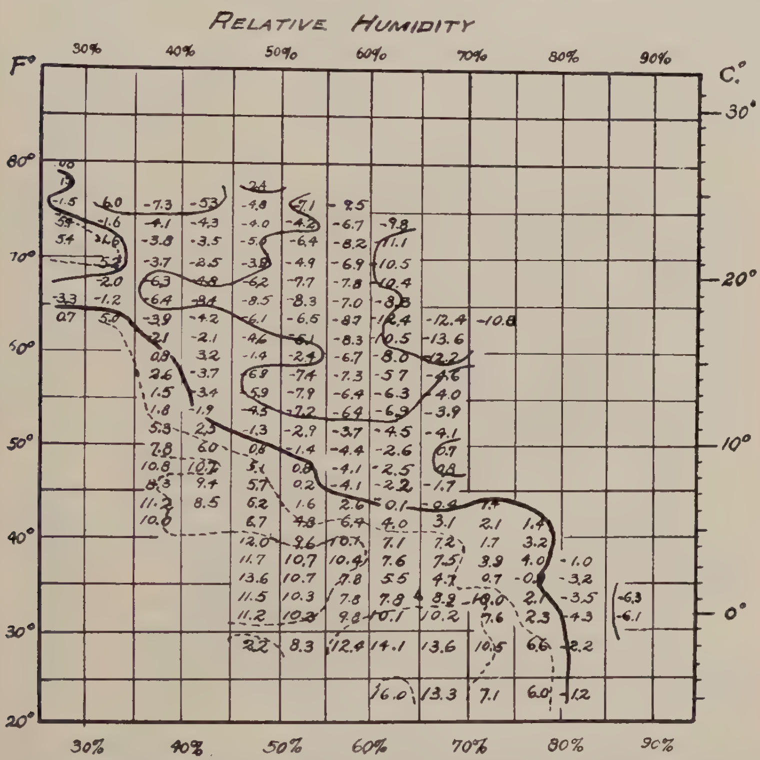


FIG. 118. Death rate in the dry interior of the United States on days with the various mean humidities and temperatures plotted (after Huntington (419)). The death rate is measured in per cent above normal (+) and below normal (−). Lines are drawn through equal death rates and are not smoothed.

most favorable conditions) was 60 per cent. In other words, the time of death was influenced by weather in 60 cases out of 100, while in the other 40 cases death was due to accidents, etc., entirely independent of weather. On this basis, relative survival has been plotted in figure 120 on a vertical scale of 60 units, on which the zero point represents the death of all (i.e., the survival of none) of the 60 persons

who would survive if conditions were as favorable as possible. Each curve shows the survival data at various temperatures for the indicated per cent humidity. The curve for 40 per cent humidity was drawn in harmony with the others on the basis of the concept that

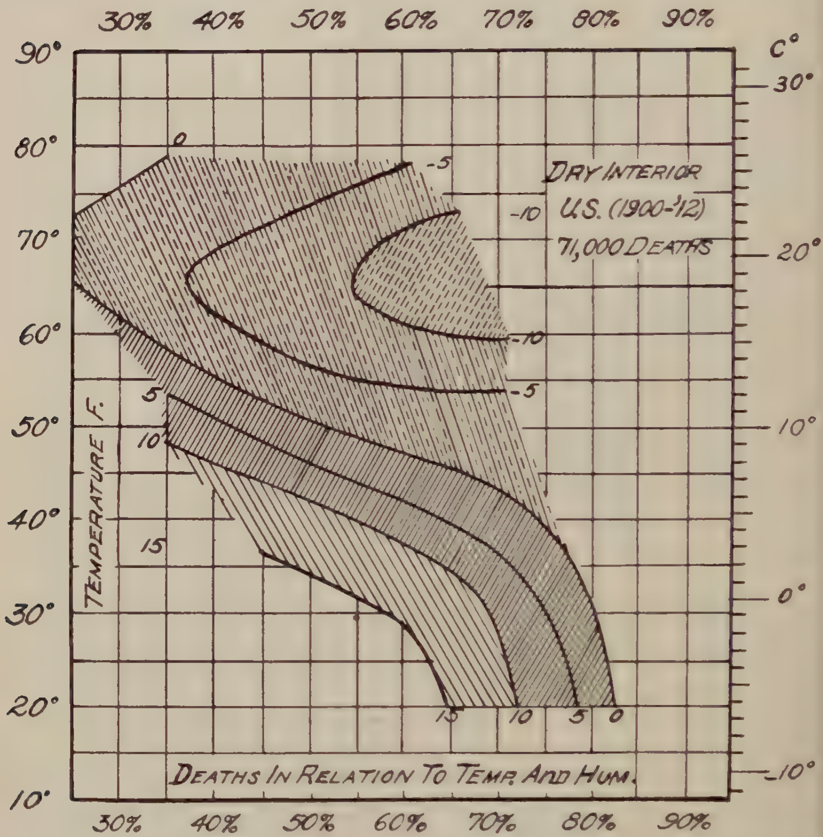


FIG. 119. Smoothed curves for the data shown in figure 118 (after Huntington (419).

the curves in figure 120 are vertical sections of a solid of which figure 121 shows the contour lines.

In the preparation of figure 121 the relative survival values shown by the curves in figure 120 were plotted on a temperature-humidity chart, and lines were drawn through points of equal survival values

at 5-unit intervals; these lines were then smoothed and additional lines were drawn in harmony with them, so as to give a complete generalized picture of the relationship. Such a diagram is three-dimensional: length and width are temperature and humidity, and thickness is relative survival. Each equal-survival line should be

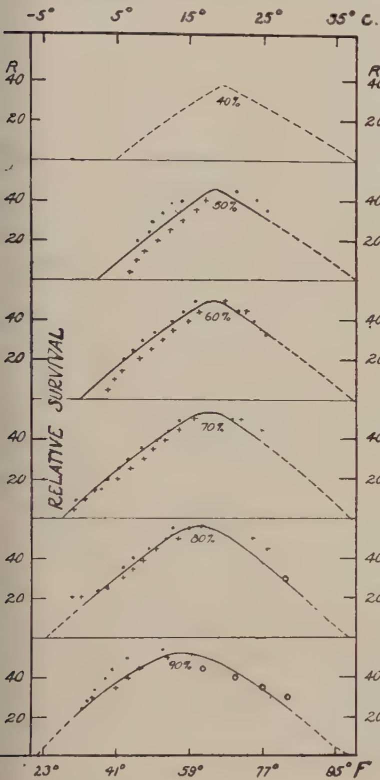


FIG. 120

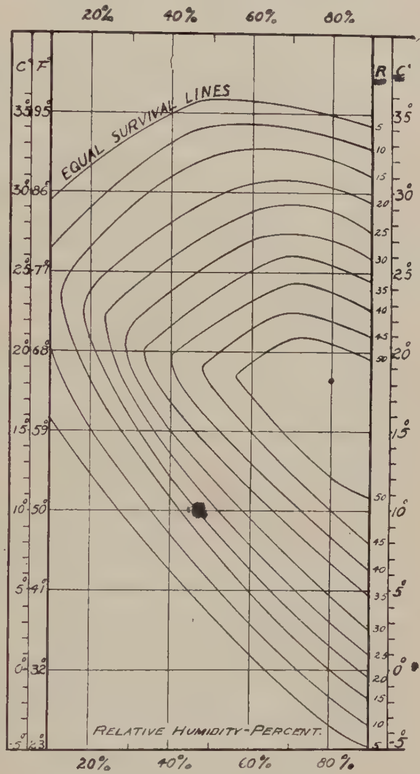


FIG. 121

FIG. 120. Combined and generalized curves of survival rates in southeastern United States (○), southern France (+) and northern Italy (●).
FIG. 121. Shows the curves combined in a chart similar to figure 119.

thought of as being at its proper elevation above the temperature-humidity base. The figure is like a map of a mountain, with contour lines representing levels of survival. (Cf. figure 119, in which a great number of records made possible the drafting of an equal death rate chart (figure 118) directly from the data.)

To illustrate the use of this chart, take from table 25, page 282, the mean temperature and humidity for a certain spring day in Illinois; 10° and 47 per cent. On figure 121 the point corresponding to this temperature-humidity combination is found to fall on the equal-survival contour line which has a value of 20, which indicates that 20 of the 60 persons influenced by temperature and humidity survive that day.

III. VELOCITY OF DEVELOPMENT

1. *Velocity in relation to temperature and humidity*

A set of relative velocity curves for a full series of humidities, 10 per cent apart, based on the same humidity throughout each curve, is shown in figure 122. Full instructions as to the method of constructing such curves are contained in Chapter VII. Each curve represents the ideal results of a set of experiments at the humidity indicated. These curves are based upon most of the knowledge available as to rates of development of insects and other cold-blooded land animals. The form of the curves outside the medial temperatures is based largely on the writer's experience with the codling moth pupae and eggs (826, fig. 13, p. 384) and larvae after dormancy is broken, as shown in figure 130. The work of Sanderson and Peairs (774), Krogh (498, 499) and Headlee (380, 381), and Hefley (382) had an important influence on the form we have given these curves within the medial range of temperature and just outside this range. The developmental units (here plotted on the vertical scale) are derived from the reciprocal of the mean time required to complete stages of the life cycle under different given conditions. These curves are the starting point for constructing an equal-velocity chart comparable to the equal death rate chart shown in figure 119 and the equal-survival chart shown in figure 121. Figure 130 shows how thinly a fairly good set of experimental results covers such a chart and indicates some of the difficulty which might be encountered in making such a chart from the plotting of reciprocals directly (fig. 118). Accordingly, from the curves in figure 122, which represent cross sections of a "mountain" of velocity, contour lines representing levels of equal velocity were drawn as shown in figure 124. The curves in figure 122 were laid off on coördinate paper (one block equal 5°C. and 20 per cent humidity) by marking the temperature on which

velocities of 0, 1, 2, 3, 5, 10, 15, 20, and 25 occur along 100 per cent, 90 per cent, 80 per cent, etc. When this had been done for all the curves the same velocity numbers were connected with lines as

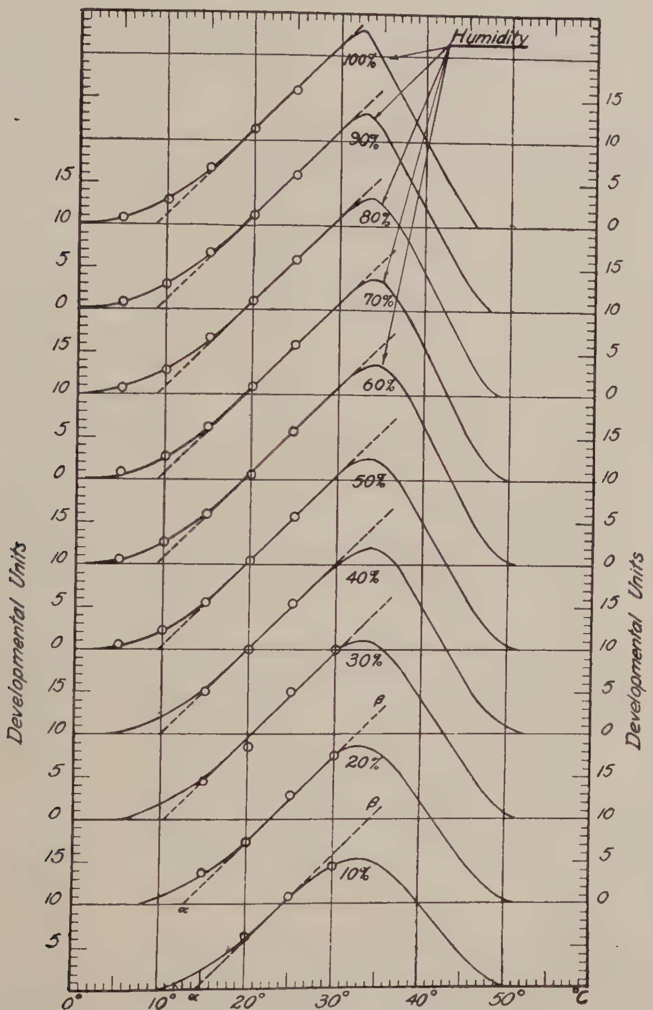


FIG. 122. Shows idealized velocity curves representing a mean for all land poikilotherms for which there are records. The curves are drawn to represent the rate of development at humidities (10 to 100 per cent) by 10 per cent intervals.

shown in figure 124. Lines were then drawn properly dividing the intervals between the lines already established.

These curves in figure 122 are indicative of results of experiments run at various temperatures (see Chapter VII) and the *same* humidity, which was approximately the method employed by the writer in work on the codling moth (826). In actual practice it was necessary to smooth the equal-velocity lines resulting from transferring velocity curves similar to those shown in figure 124 because the original curves were irregular, as shown in figure 123. The equal-velocity lines found are shown as dotted lines and those resulting from smoothing are shown as solid lines. The evidence in hand in this case indicated that smoothing was necessitated by the heterogeneity of material

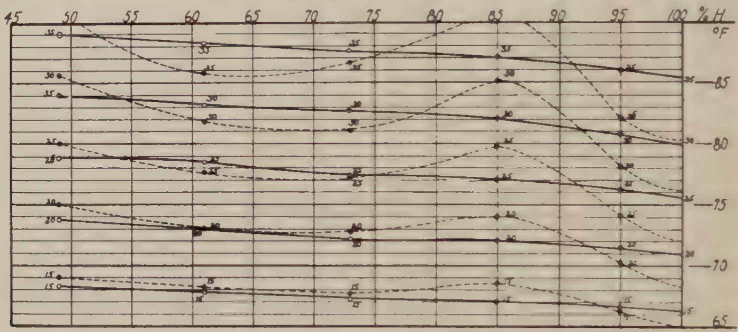


FIG. 123. Method of smoothing velocity curves. Velocities from curves similar to those shown in fig. 122 are indicated by dots. The broken lines were drawn connecting these dots, and the solid lines were then drawn by smoothing these lines to bring them into harmony. Temperature in °F.

used. It was drawn from several generations and represented different water treatments, food qualities, and general weather conditions. There is no reason to believe that uniform stocks would show this irregularity. The results of Krogh on *Tenebrio* are very regular. A better method will also be presented in a succeeding paragraph.

2. Life limits and daily march of temperature and humidity

The chart shown in figure 125 is useful in bringing out several facts relative to organisms and weather. First, with reference to organisms: in figure 125, which shows equal-velocity lines at 5-unit intervals traced from figure 124, the oblique shading covers combina-

tions of constant temperature and humidity which are unlikely to produce complete development of animals native to temperate regions; i.e., the animals are quite sure to die before development is

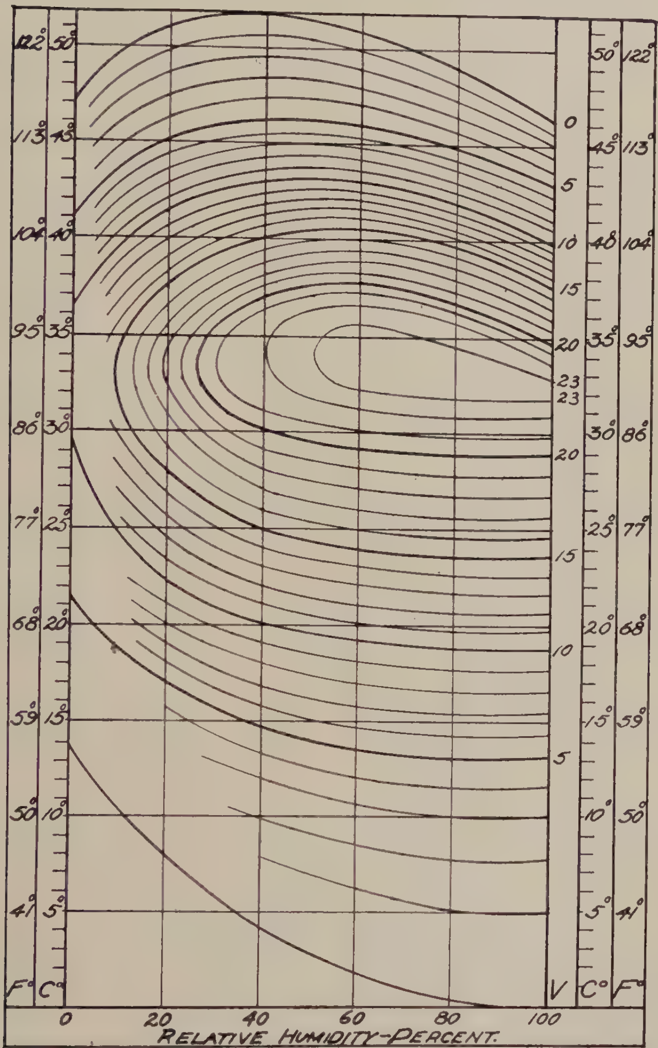


FIG. 124. An idealized equal-velocity chart for all tempeatures from 0° to 52°C. and relative humidity from 0 to 100 per cent saturation. The chart represents mean values for all known data. Drawn from fig. 122.

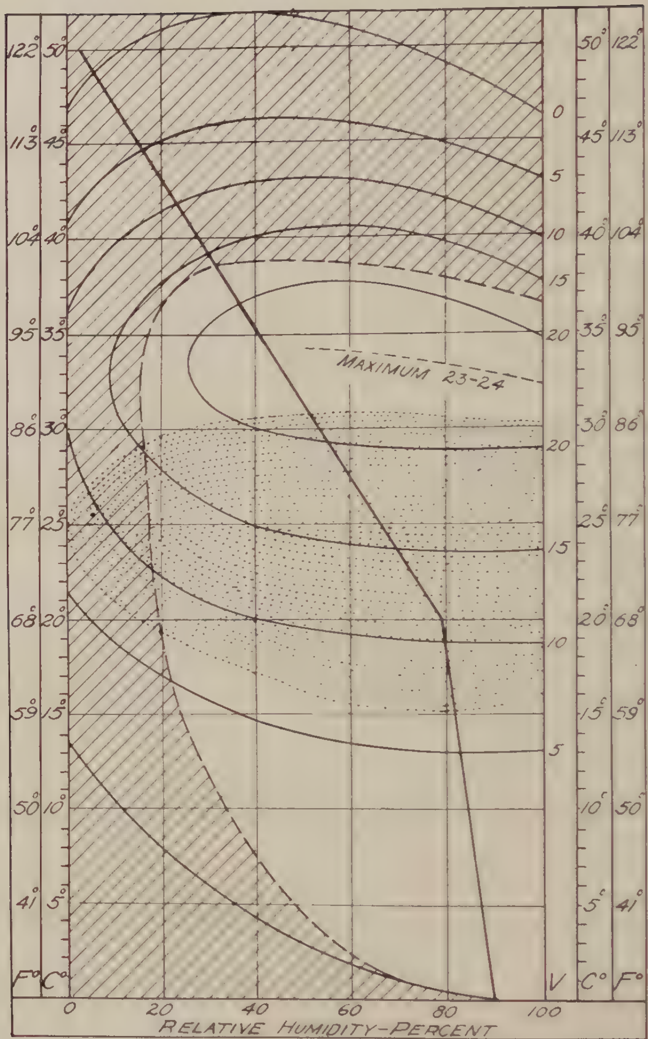


FIG. 125. The same as figure 124 but with details omitted. The average daily temperature and humidity march for Olney, Illinois, is represented by a heavy oblique line. The shaded area covers combinations of temperature and humidity under which survival is unlikely under constant temperatures. Medial temperatures and humidities are indicated by stippling.

completed. Again, with reference to the weather, there has been added to this figure a heavy oblique line running from 90 per cent humidity on 0°C. to 50°C. approaching zero humidity, which represents the average daily march of temperature and humidity in south-central Illinois for spring and summer of the years 1915, 1916, and 1917. *Climate-simulation experiments on animals native to this region should be arranged in accord with this "line of march."*

Combinations of temperature and humidity represented by the oblique lines in figure 126 should be chosen for this purpose. The successful completion of a series of experiments under *constant* conditions as indicated by the 65 dots on this figure, would lay the foundation for a chart showing rate of development for the species studied. This chart should then be modified according to the results of a second series of experiments using *variable* temperatures within the medial range of conditions indicated by the stippled area in figure 125. (The stippling covers the temperatures within which the velocity curve is approximately a straight line.) Such experiments are likely to show a correct *alpha* and a constant time-temperature relation for variable temperatures out of doors. It is very important to make a third series of experiments with variable temperatures ranging into and out of the combinations covered by the stippling in figure 125, so as to supply data for the upper and lower ends of the velocity curve. These three series should be run with uniform material, i.e., with the same generation of the same stock, in order to eliminate variations in rate of development due to differences in storage conditions or in weather conditions under which the animals had been living.

3. A comprehensive plan for experiments (824)

The methods of experimentation for the determination of weather influences should be so arranged as to give a fairly complete set of combinations of temperature and humidity on uniform stock. The following series will usually need to be made:

a. Constant temperature experiments. At two- to five-degree intervals from 5°C. to 39°C. with humidities of 45, 55, 65, 75, 85, 95, and 100 per cent arranged in a series in accord with the dots placed in figure 126.

b. Variable temperature experiments. (a) With variations within the medial range of temperature (18° to 29°C.) starting with humidi-

ties of 90, 80, 70, and 60 per cent at 18°C. as suggested in figure 126. (b) With variations outside the medial temperatures, such as:

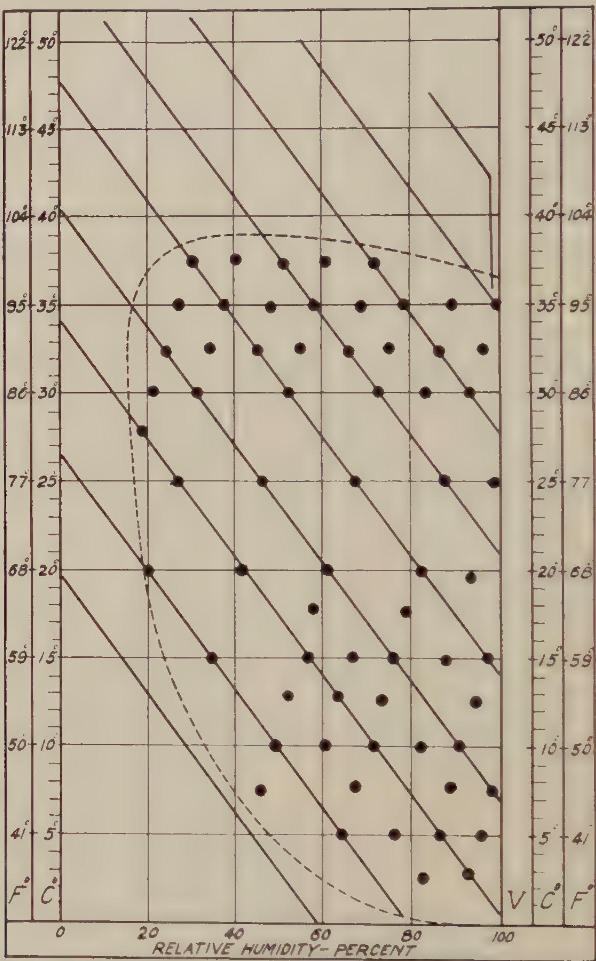


FIG. 126. Shows by oblique lines the approximate variation in temperature and humidity that should be followed in variable-temperature experiments. The large dots indicate the combinations of temperature and humidity at which the experiments should be run.

from 27° to 47°C. starting at 100, 60, 40, and 30 per cent humidity; and from 0° to 20°C. starting at 100, 80, and 60 per cent humidity;

also with several other combinations extending outside the limits of life for the species (fig. 125) but within the limits of possible weather conditions as suggested by the dots in figure 126.

c. Outdoor observations. With animals in experimental containers

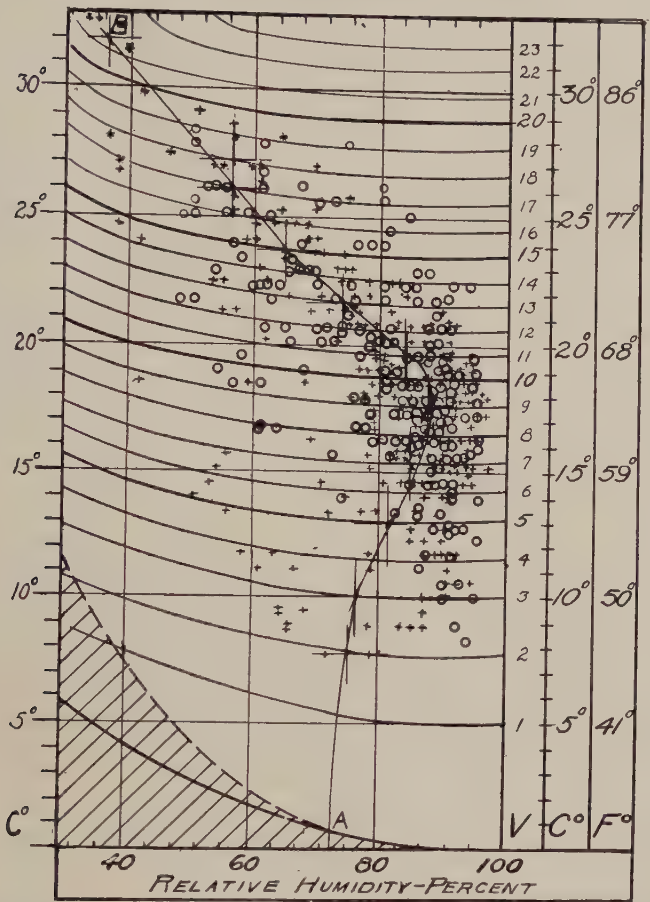


FIG. 127. A portion of the chart shown in figure 126, with crosses showing the bi-hourly temperature and humidity readings from hygrothermograph record sheets for May 14 to June 4, 1915, at Olney, Illinois, and circles showing similar readings for August 17 to September 3, 1915, at the same place (data by P. A. Glenn). The sinuate line *AB* indicates the mean daily course of humidity and temperature May 14 to June 4. It passes through the mean temperature, humidity, and velocity points shown by the large crosses at intervals of two velocity units (1–2, 3–4, 5–6, etc.). (See Figs. 128 and 130.)

placed out of doors and, if possible, with air movement produced by wind.

Such a program of experiments requires 6,000 to 10,000 individuals in each life-history stage, and several men to carry on the work. The experiments should be repeated during each of two or three years, if possible. If not, at least one year's work should be on the

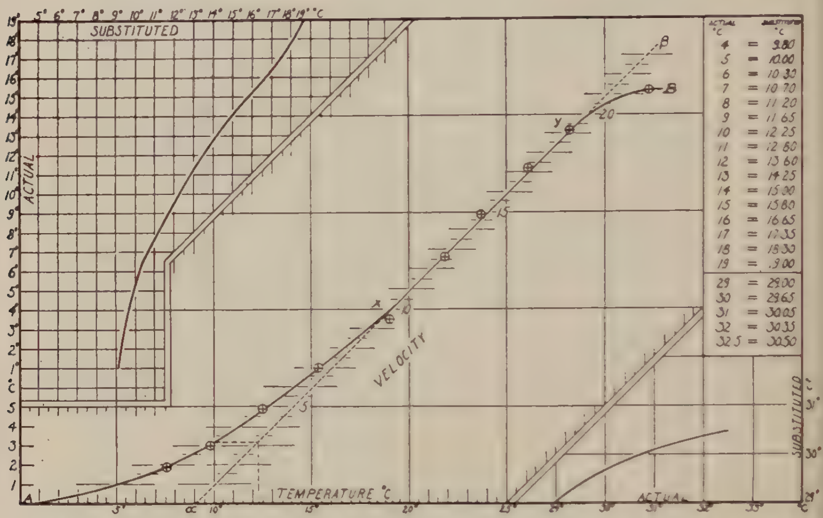


Fig. 128. Temperature-substitution method for expressing velocity in developmental units per hour. The mean velocity values indicated by the small crosses on figure 127 are here plotted on their respective temperatures and give the curve AB. The constant for the straight-line portion (xy) of this curve may be determined by summing the hourly temperatures (or twice bi-hourly temperatures) within the straight-line limits and by substituting for all temperatures outside these limits other temperatures having the same velocity values. In substituting, a temperature *on* the straight line and of the *same* velocity as the temperature read is used; thus, following up from 10° to the curve, then to the right to the dotted line and downward, it is determined that 12.25° should be substituted for 10°. Actual and substitution curves and tables derived by this method are adjacent.

scale suggested, and a smaller number of experiments in subsequent years should be made for comparison. Otherwise, the difference in stock used will throw much irregularity into the results and greatly increase the difficulty and error with eventually no saving of expense.

d. The construction of equal-velocity charts. The purpose of this work is to establish a chart of the type shown in figures 121, 124, and

130 and which may be adjusted to actual weather conditions. The chart given in figure 130 is shown as made (except for transposition into centigrade (fig. 27, p. 415, Shelford (826)) in an attempt to determine the rate of development of the hibernated codling moth larvae in the pre-pupal stage, i.e., after the breaking up of dormancy. The essential data on which the chart was based are added in place on the chart. It was drawn from a series of velocity curves (fig. 26, p. 414, Shelford (826)) similar to those shown in figures 120 and 122.

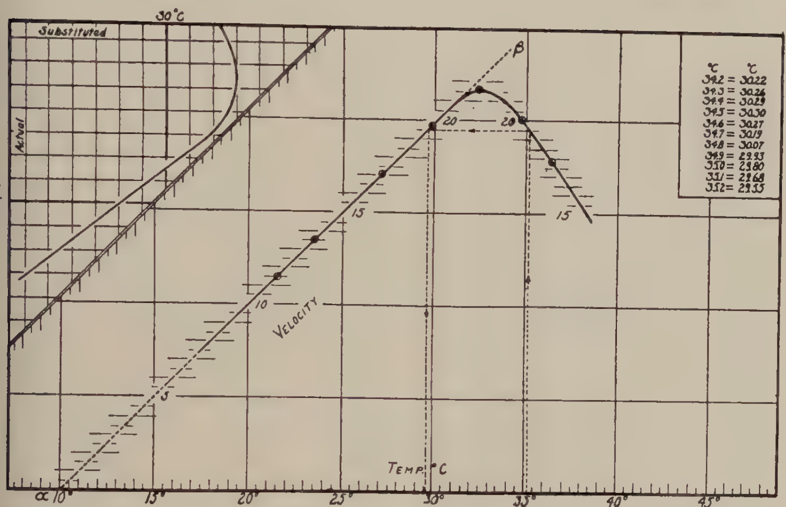


FIG. 129. Corrected velocity curve for a group of codling moth pupae pupating at Olney, Illinois, August 1 and emerging August 10, 1916 (data by P. A. Glenn); a typical hot weather curve not use in the text discussion. The weather data were plotted on a trial chart (Shelford (27)) similar to figure 124 and as shown by circles in figure 127, and mean velocity values are plotted here on mean temperatures.

The attempt to complete and utilize the chart was discontinued because of lack of data and lack of knowledge of the time of breaking of dormancy.

Table 25 shows the mean hourly temperature and mean hourly relative humidity for the same hours, during one spring day in Illinois. In column 4, opposite these temperatures and humidities, are the velocities in developmental units per hour read off the chart shown in figure 130; the total of these for the day is 45.3. In column 5 are the developmental units per hour for the same combinations

TABLE 24

Showing velocity values transcribed from figure 124

TEMPERATURE	PER CENT HUMIDITY								
	20	30	40	50	60	70	80	90	100
°C.									
52		0.0	0.0	0.0					
51	0.0	0.6	0.9	0.6	0.0	0.0			
50	1.2	1.4	1.6	1.5	1.0	0.2			
49	1.7	2.3	2.6	2.4	2.0	1.2	0.0		
48	2.5	3.1	3.3	3.3	3.0	2.2	1.2	0.0	
47	3.5	4.0	4.3	4.3	4.0	3.3	2.5	1.0	0.0
46	4.3	5.0	5.3	5.2	5.0	4.4	3.6	2.3	0.5
45	5.2	6.2	6.8	7.0	6.6	5.8	4.7	3.6	2.0
44	6.5	7.7	8.3	8.5	8.3	7.5	6.4	5.0	3.5
43	8.2	9.0	10.0	10.0	10.0	9.0	8.0	6.5	4.9
42	9.0	10.5	11.6	12.0	12.0	11.0	10.0	8.0	6.5
41	10.5	12.0	13.3	14.0	14.0	13.0	12.0	10.0	8.0
40	12.0	13.6	15.0	15.8	16.0	15.5	14.3	12.0	9.7
39	13.0	15.2	16.6	17.3	17.7	17.2	16.2	14.5	12.0
38	14.5	16.4	18.0	19.0	19.5	18.9	17.7	16.2	14.0
37	15.6	18.0	20.0	21.0	21.5	21.0	19.5	18.0	16.0
36	16.5	19.0	21.2	22.0	22.6	22.2	21.5	19.5	17.6
35	17.5	20.4	21.8	22.6	23.5	23.2	22.6	21.5	19.2
33	18.3	20.2	21.8	22.6	23.5	23.6	24.0	23.8	22.6
31	17.0	19.3	21.0	21.5	21.8	22.0	22.3	22.3	22.2
29	16.3	17.5	19.0	19.5	20.0	20.0	20.1	20.1	20.1
27	14.0	16.0	17.0	17.5	18.0	18.2	18.3	18.3	18.2
25	12.5	14.0	15.0	15.6	16.0	16.3	16.4	16.5	16.4
23	10.7	12.0	13.0	13.6	14.0	14.3	14.5	14.6	14.5
21	9.0	10.0	11.0	11.6	12.0	12.3	12.5	12.5	12.5
19	7.0	8.0	9.0	9.5	9.8	10.1	10.3	10.2	10.2
17	5.0	6.0	7.0	7.7	8.0	8.2	8.4	8.5	8.4
15	3.5	4.4	5.3	6.0	6.3	6.5	6.6	6.7	6.6
14	2.5	3.7	4.5	5.0	5.5	5.7	5.8	5.8	5.8
13	2.0	3.0	3.8	4.3	4.6	5.0	5.0	5.0	5.0
12	1.6	2.5	3.0	3.5	4.0	4.2	4.3	4.2	4.3
11	1.0	1.9	2.5	2.9	3.3	3.6	3.7	3.7	3.8
10	0.6	1.3	2.0	2.4	2.6	2.9	3.0	3.0	3.0
9	2.3	1.0	1.5	1.9	2.2	2.4	2.6	2.6	2.6
8	0.0	0.5	1.0	1.5	1.8	2.0	2.2	2.2	2.2
7		0.1	0.8	1.0	1.3	1.5	1.8	1.8	1.7
6		0.0	0.5	0.7	1.0	1.2	1.4	1.5	1.4
5			0.3	0.5	0.7	0.9	1.0	1.0	1.0
4			0.0	0.3	0.5	0.7	0.8	0.8	0.8
3				0.0	0.3	0.5	0.6	0.6	0.6
2					0.0	0.2	0.3	0.4	0.4
1						0.0	0.2	0.2	0.2
0							0.0	0.0	0.0

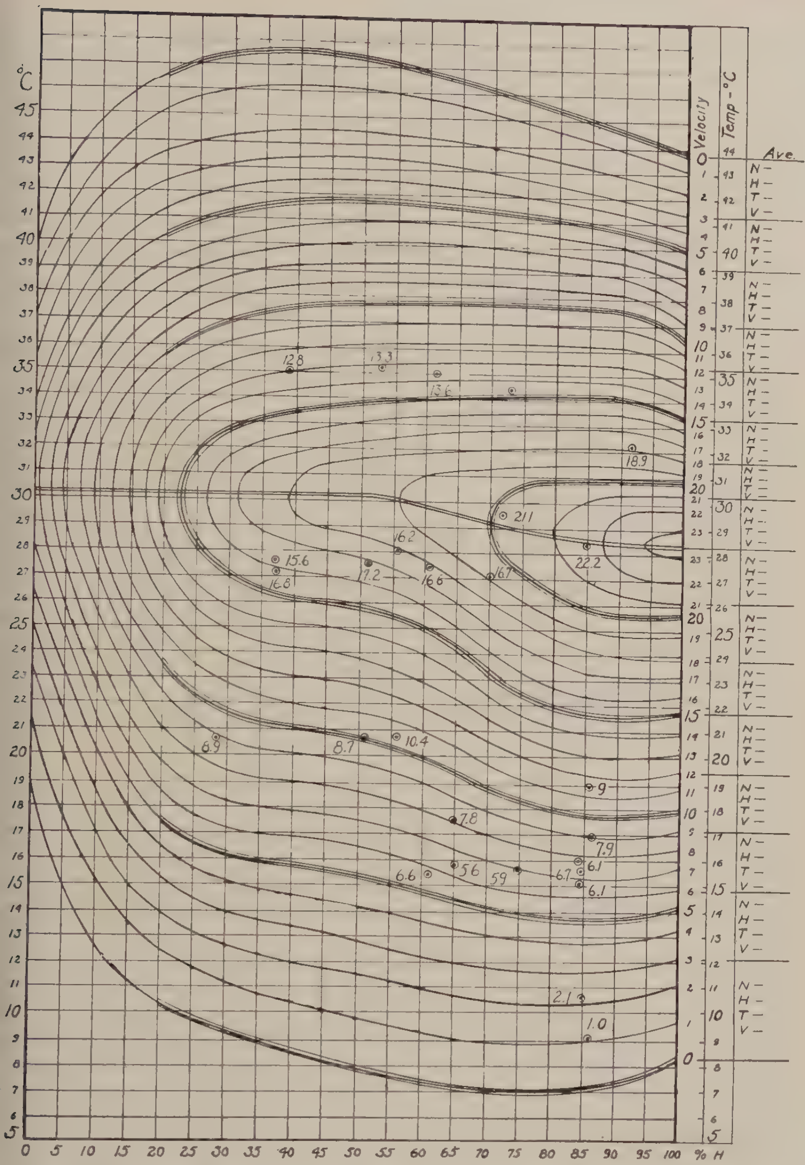


FIG. 130. Shows a trial velocity chart for the prepupal stage of the hiber-
ated codling moth larvae with the experimental (constant-temperature)
ata on which it was based shown by dots in circles with the velocities adjacent.
Each velocity unit is 1/2420th part of the total development required to
omplete the prepupal stage. The letters on the right are to indicate records
f number of items, relative humidity, temperature and velocity in case the
hart is used for recording and averaging weather data (see fig. 127) for ve-
ocities between the three spaces opposite the long lines (see fig. 128 and
able 26).

of temperature as read from the chart shown in figure 124, which is a composite chart representing roughly the mean for a number of

TABLE 25

Mean hourly temperature and mean hourly relative humidity for the same hours

(1) HOUR	(2) TEMPERATURE	(3) HUMIDITY	(4) VELOCITY, FIGURE 130	(5) VELOCITY, FIGURE 124	(6) TEMPERATURE SUBSTITUTED, FIGURE 128	(7) CORRECTED DEGREES ABOVE 9°
	°C.	*per cent saturation*				
1:00 p.m.	17	30	5.8	6.0	17.35	8.35
2:00 p.m.	16	33	5.0	5.5	16.65	7.65
3:00 p.m.	16	30	4.9	5.3	16.65	7.65
4:00 p.m.	15	34	4.1	4.8	15.80	6.80
5:00 p.m.	14	35	3.3	4.0	15.00	6.00
6:00 p.m.	13	36	2.5	2.4	14.25	5.25
7:00 p.m.	10	50	1.1	3.3	12.25	3.25
8:00 p.m.	8	66	0.3	1.8	11.20	2.20
9:00 p.m.	7	68	0.0	1.5	10.70	1.70
10:00 p.m.	6	70	0.0	1.1	10.30	1.30
11:00 p.m.	7	62	0.0	1.2	10.70	1.70
12:00 p.m.	7	57	0.0	1.2	10.70	1.70
1:00 a.m.	6	49	0.0	0.8	10.30	1.30
2:00 a.m.	6	42	0.0	0.4	10.30	1.30
3:00 a.m.	5	41	0.0	0.2	10.00	1.00
4:00 a.m.	4	40	0.0	0.0	9.80	0.80
5:00 a.m.	5	41	0.0	0.2	10.00	1.00
6:00 a.m.	6	42	0.0	0.4	10.30	1.30
7:00 a.m.	7	44	0.0	1.0	10.70	1.70
8:00 a.m.	8	47	0.0	1.2	11.20	2.20
9:00 a.m.	11	52	1.7	2.8	12.80	3.80
10:00 a.m.	14	58	4.2	5.3	15.00	6.00
11:00 a.m.	15	60	5.2	6.3	15.80	6.80
12:00 m.	17	62	7.2	8.0	17.35	8.35
	Mean 10	47	Sum 45.3	64.7	Mean 12.71	Total 89.10
	$\frac{20}{60}$		$\frac{45.3}{2420.0}$		Substitution quotient 89.1/24 = 3.71	

insects. The developmental sum (page 369) for this day is 64.7 units—due to development indicated at low temperatures (where zeros show in column 4) which characterizes some species.

IV. CHECKING EQUAL-VELOCITY CHARTS

When a trial equal-velocity chart has been developed from experimental data, it can be checked against *known weather conditions.* Hourly or bi-hourly temperature and humidity readings and known lengths of stages of the organisms being studied are essential records. Such records should extend over at least two years; three years would be better, because more variation would be shown. The weather records should be as inclusive as possible throughout the period in question and should begin with the hibernation of the generation in the winter preceding the summer's experimentation.

1. Calculated-time method

The first and simplest method consists in comparing the actual time taken to complete stages with the time which may be calculated from the chart. If the time calculated by use of the chart agrees with the actual time, the chart is probably nearly correct.

To illustrate this method table 25 shows in the first three columns the mean hourly temperature and humidity for a typical spring day. Turning to figure 130 and locating the point of intersection of humidity 30 with temperature 17, it is found to agree with velocity 5.8; 33 per cent and 16°, agree with velocity 5.0, etc. Turning to figure 124, velocities 6.0 and 5.5 are found to agree with these two temperature-humidity combinations.

With figure 130 the sum of developmental units for the day is 45.3. In this case (approximate), this is 45.3/2420.0 of the prepupal period. If the chart and final sum are correct, pupation would take place after about 53 similar days, or when the sum for all the days approximated 2420.

With the use of figure 124 a sum of 64.7 developmental units is found for the day. Here no developmental total is assumed. It is likely to range from 2000 to 12,000 depending on the stage or species.

The tedium and uncertainty of reading velocities directly from the chart is evident. They should be read off from the chart and recorded in the form of a table once for all. Such a set of figures for large intervals is shown in table 24. Such a table in full detail is essential to checking by this method.

When there is no agreement between the calculated and actual time with a variety of weather records for a chosen item, such as

the completion of the pupal stage of an insect, the chart needs correction. If it is wrong only when low temperatures prevail, or when only high temperatures prevail, these parts of the chart are probably wrong and other parts right.

2. The substitution method

A second method of checking a chart is the substitution method. No table of velocities need be made. The chart must be completed in tentative form on tracing cloth and "Vandyked" and positive blueprints provided as shown in figure 130, but with the experimental data omitted, or as shown in figure 124, but with blanks for data similar to those at the right of 130. Hourly or bi-hourly readings of temperature and humidity are prepared from hygrothermograph records as shown in table 24 (first three columns) for the entire season or seasons in which records of duration of stage are available under actual weather conditions.

It has been found that bi-hourly readings may be used instead of hourly means without materially changing the end results.

The bi-hourly readings for the period of a known stage are placed on the chart as shown in figure 127, where the crosses are for the period May 14 to June 4 and the circles for August 17 to September 3, 1915, at Olney, Illinois (826).

The large crosses represent the mean velocity, mean temperature and mean humidity for the weather data. Table 26 shows the means as transcribed from the small crosses on figure 127. The data in columns 2 and 3 are embodied in the curve in figure 128. The alpha value is determined by prolonging the straight line drawn through the velocity and temperature points represented by the circles with enclosed crosses. The number of items giving the mean velocity and mean temperature is useful in locating this line as it permits giving the proper weight to each point.

a. Substitution—graphic method. In carrying out the process referred to as *substitution*, temperatures falling in the concave range of the curve at the lower end and in the convex range at the upper end, are thrown out. Temperatures with the *same velocity* value but falling on the straight line $\alpha-\beta$ are substituted. The inserted curves and tables in figure 128 show the values to be substituted. The long list of temperatures from May 14 to June 4 (bi-hourly readings) must be gone over and substitutions made for all tempera-

tures outside the straight line limits or medial temperatures, that is, below 18° and above 29°C. (see table 25). The alpha temperature, or 9°, is then subtracted from all actual temperatures and substituted temperatures as shown in table 25 last column. The remainders are then added together, and since two-hour periods were used the total must be multiplied by two to give the *substitution total.* This should correspond to the developmental total or sum of developmental units. Twice the actual total in this case is 2327. This is a set of composite rates. The codling moth rates showed a total of 3826 for pupae covering this period.

TABLE 26

Means as transcribed from the small crosses on figure 127 (see fig. 128)

VELOCITY LIMITS	MEAN VELOCITY	MEAN TEMPERATURE	MEAN HUMIDITY	NUMBER OF BI-HOURLY READINGS
1–2	1.9	7.5	75	2
2–4	3.0	9.8	77	21
4–6	4.8	12.5	82	23
6–8	7.0	15.5	87	45
8–10	9.5	18.7	89	46
10–12	11.0	19.7	84	33
12–14	12.6	21.8	75	35
14–16	14.9	23.8	64	20
16–18	17.3	26.1	56	18
18–20	19.2	28.2	56	6
20–22	21.2	32.2	35	3
Total				252

Figure 129 gives the substitution curve for the bi-hourly reading from August 17 to September 3 shown in figure 127 by circles. This is correct whether the curve takes an angle of 45 degrees or not, because the substitutions are independent of the angle (see Chapter VII, fig. 73).

A series of such operations indicates the *constant* Substitution Total for weather conditions. Dividing by 24 gives the *Substitution Quotient* which may be compared with sums of daily effective temperatures. The constant thus derived for all items of the codling moth pupa for three seasons was made up for all known data and found to be 3600°C.-hour-units on the average. The values in a chart based

on constant-temperature experiments are likely to require multiplication by 1.07, or a figure of similar magnitude, to correct for the acceleration due to variability.

b. Tabulation method. A third method, which is the second method of accomplishing substitution, does not require the manifolding of the chart, but does require the making of a table similar to that in table 24, but in full detail covering temperatures in half degrees and humidities in 2 per cent intervals. Such a table may be divided into two-unit intervals. The temperature and humidity hourly or bi-hourly readings and their corresponding velocities may then be arranged and in these classes. Thus turning to table 25 the class velocities 0 to 2.0 (fig. 124) would include all readings from 8:00 p.m. to 8:00 a.m.

TABLE 27

Summation in segregated groups of two velocity limits

VELOCITY LIMITS	NUMBER OF ITEMS	TEMPERATURE		VELOCITY	
		Sum	Mean	Sum	Mean
0–2	13	92	7.0	11.0	0.84
2–4	3	34	11.3	8.5	2.8
4–6	5	75	15.0	24.9	5.0
6–8	2	32	16.0	12.3	6.1
8–10	1	17	17.0	8.0	8.0

When summed in segregated groups of two velocity limits the results appear as shown in table 27 (use columns 2 and 5). Such a table must be made for each day and a daily total of units found. These are then added together covering the period in question, to give a final sum for the stage. In any actual stage at this temperature the period would be ten days or more, so that final sums would be large. The advantage of this plan lies in the fact that a stage beginning a day later and ending a day later may be readily calculated merely by subtracting the total for the first day and adding that of the day following the last, to the grand total for the preceding stage.

The mean temperatures and velocities obtained by this method may be used to plot curves (figs. 128 and 129) to form the basis for substitution just as those obtained by the other method.

The final purpose of the substitution method is to prepare a table of developmental units adjusted to the average weather conditions. Such a table consists of units per hour for each 2 per cent humidity and each 0.5°C. If this table is corrected to a long series of data covering all generations in two or three years, the resulting velocity rates represent the average and may be used as a standard for all years and probably for all localities. Such a table covering the codling moth egg and pupa was made by the writer (826).

V. VARIATION IN PHYSIOLOGICAL CONDITION AND RESPONSE

Sanderson (772) and Headlee (381) have called attention to differences between different generations in respect to responses. These differences, together with differences from year to year, have also been brought out by the writer's studies of the codling moth and chinch bug under the auspices of the Illinois Natural History Survey. The following are striking examples of variation, the causes of which are partly known and the experimental control of which is possible: For the codling moth, there may be as much as 20 per cent variation in the length of the pupal stage under the same conditions of temperature and humidity; the length of all stages varies with rising and falling mean daily temperature, with the generation, and with rainfall; and the threshold, or point at which development begins to be perceptible, varies from season to season. For the chinch bug, the number of generations in a year varies; and the vitality of the stock taken from the field, as shown by abundance under the same experimental conditions, varies from year to year.

Variations in time of appearance of stages are due in part to the weather of preceding seasons. This necessitates full and continuous weather records not only for the period of experimentation but also for several months or a year preceding it.

VI. PROVISIONAL STUDIES

As has been indicated, an extensive plant is essential to complete a table or to secure data showing the effect of developmental rates within a few years. There is, however, very much that can be done by single investigators with a small amount of equipment.

1. Small series of constant-temperature experiments at humidities falling on the line of daily march (see fig. 125) will give the value of alpha and the straight-line limits for average conditions.

2. Variable temperatures with variation following the average daily-march lines will give velocity values outside the straight-line limits.

3. Repetition of experiments in exactly the same way with stocks from different years and generations will show variation due to weather.

The approximate alpha value, the approximate straight-line limits, and the approximate maximum, will not vary sufficiently from time to time but that any data gathered relative to particular species will be a contribution to knowledge. The more carefully the experiments are controlled, and the more carefully the records are made of the conditions which the stock underwent before the experiments began, the greater will be the contribution.

VII. THE EFFECTS OF HUMIDITY ON SURVIVAL AND DEVELOPMENT

The effects of humidity in nature are evidently usually in correlation with effects of temperature. The effects of both are well illustrated in the velocity charts discussed in this chapter. An inspection of figures 118 to 123 will bring out the following general effects:

1. The maximum *survival* shown by Huntington for man (fig. 121) the maximum *rate* of development of the codling moth (fig. 130), the *survival* of codling moth pupae (fig. 12 in (826)) and the schematic relations brought out by Pierce for the cotton boll weevil, all shift up the temperature scale as the humidity is lowered. The same is true of each specific rate of development, survival, etc.

2. The threshold shifts upwards on the temperature scale as the humidity is lowered below 85 or 90 per cent. For some of the charts the same is true for raising humidities above 85 or 90 per cent.

For further discussion of terms and standards used in the measurement of development, see Chapter XV, pages 366–370.

CHAPTER XII

The Effect and Measurement of Air Pressure and Evaporation

I. BAROMETRIC PRESSURE

Barometric pressure has important effects upon animals. There is a large body of literature on reduced pressure: Bert (80), Mosso (606), Haldane (362), Herrera and Lope (390), and others so well known as to make an extended review of their work unnecessary. Herrera and Lope show the altitude attained by various animal groups in considerable detail; birds and butterflies attain the greatest heights.

1. Decreased pressure—altitude

Schneider has recently (783) summarized the work on the physiology of altitude. Increased oxygen consumption and carbon dioxide output, increased respiration and heart beat, in most mammals under reduced atmospheric pressure, due in the main to low oxygen pressure which reduces alveolar carbon dioxide, are well known. Guinea pigs, which are probably descended from Peruvian high mountain ancestors, do not show this effect (Hill (401)). Herrera and Lope describe decompression experiments on frogs and aquatic beetles indicating that the lower vertebrates and invertebrates are affected by the reduced pressure also.

2. Decreased pressure—storms

There are barometric pressure differences accompanying storms. A complex of factors varies, however. Evaporation, temperature, humidity and wind are changed.

a. Effects of storms upon insects. Parman (653) made observations of flies in relation to tornadoes, especially at Urvalde, Texas. The West Indian hurricane of August 18, 1916, was a typical cyclone characterized by a remarkably small diameter and an extremely steep barometric gradient. Condition of flies previous to the storm was as follows: *Stomoxys calcitrans* was very abundant and annoying stock. House flies were covering screens of houses. Five thousand

Musca domestica and *Chrysomyia macellaria* were taken in traps in forty-eight hours. After the storm, flies of all kinds were very scarce for ten or fifteen days. They did not increase much again that season although conditions seemed favorable. The storm of September 15 and 16, 1919 was similar, but the barometric gradient was not so steep or the wind so strong. Before the storm, flies were abundant. After the storm, *Haematobia irritans* was practically exterminated. The decrease in the others was as follows: *C. macellaria*, 75 per cent; *M. domestica*, 50 per cent, *S. calcitrans*, 25 per cent. The adults of all other observed species decreased in numbers to some extent. They began to increase again after fifteen days, then increased normally. Observation of flies in cages November 20–27, 1919 (653) showed the percentage of mortality of the adult *C. macellaria* to be greater under a falling barometer than under a rising barometer.

Insects attracted to lights at night (653) are more active while the barometer is rising. The bred adult Diptera tend to emerge during periods of rising barometer. Muscoid Diptera are most abundant during long periods with slight variation in barometric pressure, provided other conditions are favorable. Migration of *Lybithea bachmani* takes place after storms.

3. *High pressure*

The effects of high atmospheric pressure are also well known from many experiments and from experiences with caissons, diving bells, etc. (Haldane (362), Hill (401)). Such effects have little significance in ecology except as they concern the transfer of animals native in high altitudes to low altitudes, etc.

II. EVAPORATION (315)

The combined effect of air temperature and humidity, and of air movement and barometric pressure, is expressed by the amount of water evaporated. This fact leads to the expectation that evaporation might serve as an index of all these factors, but the attempts to use it in relation to development have not been successful. This is apparently true as regards effect on activities also, though the latter at the outset gave promise of good results (808). Air movement has important effects on dispersal (556) (see pp. 80–84).

TABLE 28

Showing the rating of the different species studied when the turnings back from the modified air and per cent of time in the two halves of the experimental cages are regarded as of equal value. The ratings were obtained from the per cent of total turnings from the halves and from the per cent of time in the halves. The differences between the two per cents in each case were added and divided by 2. When the greatest number of turnings was from the end in which least time was spent, the turnings and time are of the same sign (+ or −). Thus, the rating represents the degree of positiveness after the negative trials have been subtracted and vice versa.

SPECIES	CONTROLS		EXPERIMENTS: Evaporation Produced by						AVERAGE	
			Dryness		Movement		Temperature			
	Number	Rating	Number of experiments	Rating	Number of experiments	Rating	Number of experiments	Rating	Number of experiments	Rating
From Beech woods:										
Red-backed salamander (*Plethodon cinereus*)	10	±3.0	5	−71	2	−66	2	−82	9	−73
Sticky salamander (*Plethodon glutinosus*)	2	±7.0	1	−88	1	−82			2	−85
Ground beetle (*Pterostichus*)	1	±11.0	1	−72					1	−72
Wood frog (*Rana sylvatica*)	19	±1.5	5	−68	2	−80	2	−69	9	−72
From Oak and Beech woods:										
Millipede (*Fontaria corrugate*)	10	±6.0	6	−43	4	−55	2	−83	12	−60
Widely distributed (collected from sand dunes):										
Toad (*Bufo lentiginosa*)	9	±8.0	4	−46	2	−23	3	−27	9	−32
From dry sand dunes:										
Digger wasp (*Microbembex*)	6	±1.3	6	+6					6	+6
Spider (*Geolycosa* sp.)	7	±10.0	4	+18	2	+16	2	+12	8	+15

1. Effects of evaporation on activity

Experiments upon frogs, salamanders, centipedes, spiders, and insects were made by the writer (808). Reactions were tested in long narrow cages in which the rate of evaporation was different in the

two ends and in the center. These different rates were produced by forcing air across the different thirds of the cage, moist air across one end third, ordinary air across the middle third, and dry, warm, or rapidly moving air across the remaining third. The rate of evaporation was measured by passing the air over Livingston porous cup atmometers at the same rate as across the cage. The behavior of the animals in the experimental cage was studied and compared with their behavior in an identical control cage which contained still air. The animals sometimes turned round in the control cage when no difference in the condition of the air existed, but on the average they turned back as often when headed in one direction as when headed in another. In the cages in which differences in evaporation were maintained they turned back much more often when headed toward one kind of air than when headed toward another. As a result, more time was spent in one half than in the other. If, for example, 70 per cent of the time was spent in moist air, the animals often turned back 90 per cent of the total turnings from the dry air. Thus the animals were negative to dry air and if we subtract the percentage of positiveness, namely, 30 per cent and 10 per cent, respectively, we have 40 per cent and 80 per cent, respectively, which gives an average of 60 per cent negative to dry air. This is the mode of determining the ratings given in table 28. The ratings represent negativeness or positiveness of reaction after the trials of the opposite sign have been subtracted. Table 28 gives the rating of eight species studied in this manner.

2. Survival—The relation of evaporation effects to integuments

The animals killed by rapid evaporation fall into two distinct groups: (a) those dying with an evaporation varying from 0.07 to 5.40 cc. after an exposure varying from 5 to 165 minutes, and (b) those dying with an evaporation of 31.0 to 42.0 cc. after an exposure of from 1,300 to 2,200 minutes. The first group was made up of soft-skinned amphibians, the second of chitin-covered arthropods. Even though the arthropods were much smaller and hence had more surface per volume, they lived from 8 to 450 times as long as the amphibians. In general, there was only a rough relation between survival time and reaction among animals *with similar integuments*. Of the amphibians the red backed salamanders died in dry air in 58 minutes and sticky salamanders in 87 minutes. They are rated

respectively at −72 and −85; the toad died in 160 minutes and is rated at −32. Of the chitin-covered animals the ground beetle is rated at −72 (single experiment) and died in 1,300 minutes; the the millipede at −60, died in 1,830 minutes; the spider rated at +15, died in 2,200 minutes.

3. Habitat groups

The ratings given in table 28 clearly fall into two groups which are habitat groups. The salamanders, millipedes and ground beetles (−60 to −85) were taken from the surface of the ground under the leaves in a primeval beech forest; the spiders and wasps (+6 to +18) are regular residents of the driest open sand areas. The toad is an incidental resident of the sand area. A relation exists between habitat and survival time but it is confined to animals with similar integuments. No such relation exists when one entire habitat group is compared with the other habitat group. Omitting the toad we find that the regular breeding residents of the two habitats (beech woods and open dunes) differ in kind and degree of reaction in a manner comparable with the difference in physical conditions of the habitats.

A further comparison of the different species given in the table shows important relations to vertical conditions or forest developmental stages (Yapp (994), Sherff (834), Fuller (316)), evaporation being least in the ground and at the forest floor, increasing rapidly vertically. The wood-frog spends much of its time during the day hopping about the forest floor. The red-backed salamander lives more of the time beneath the leaves and is clearly more sensitive to evaporation. The sticky salamander occurs in numbers in the beech woods proper only in moist seasons. Ordinarily it is confined to ravines where Fuller (317) found the average evaporation per day for the season to be 1.5 cc. less than at the surface of the forest proper. Since the sticky salamander occurs in moister situations than does the red-backed, the difference in the sensitiveness of the two species is related to habitat. The habits of the ground beetles are not well known; the species studied seem to be regular inhabitants of moist woods. The millipedes, while common in beech woods, are still more common in oak-hickory woods where evaporation is 1 cc. per day greater. The millipedes are less sensitive to evaporation than the ground beetles. The reaction of the spiders and wasps is in

accord with the high rate of evaporation in the sand dunes which they normally inhabit. The animals studied reacted to differences in evaporation, whether they were produced by *movement*, *dryness* or *heat*, though it is by no means demonstrated that it is *evaporation* to which the animals react. Forest (low evaporation) animals turn away from air of high evaporating power, and show a preference for air of low evaporating power. Sand dune (high evaporation) animals turn away from moist air and show a slight preference for air of high evaporating power. Thus the *type of reaction is definitely related to the usual habitat of the animals.* Furthermore, *all* the animals from a given habitat subjected to the tests, were found to be in *agreement* in reaction though there was *no general agreement* in the length of *time required to kill* them by desiccation.

a. Effects of physiological conditions involving water withdrawal. The work on the physiological effects of evaporation from the bodies of animals has been confined chiefly to the warm-blooded domestic animals and man. The loss of water from the human body was early noticed by Hippocrates and by Galen. Tiedemann described the symptoms of great thirst experienced by travelers in the desert. The first thirst is followed by dryness and smarting of the throat; next the respiratory action is increased and later long deep breaths alternate with hiccoughs; hoarseness occurs and is followed by loss of speech; the pulse is quickened; the skin becomes dry; the muscles become weak and a feeling of great fatigue ensues with staggering and labored movements. The thirst then becomes maddening and loss of consciousness usually follows soon. Rowntree (750) has summarized the water balance data for man and mammals.

Some of the early experiments in physiology were water starvation experiments on birds and mammals. Nothwang (628) summarizes this early literature. He states, on the basis of his own investigations, that fat animals resist lack of water better than those without fat. Weyrich (970) studied the loss of water from the body and confirmed the work of earlier writers; Reinhard (726) found that the water loss was dependent upon *temperature*, *humidity*, *wind velocity*, and *pressure*. These factors control evaporation (Erismann, 279). Rubner (753) found that the rate of evaporation was of much importance in connection with the factors pointed out by Reinhard, in determining the rate of *metabolism*, and general heat *regulation economy* in men and dogs, and with Cramer (808), noted the effect

of hair covering and of sunlight upon water loss and heat regulation. Schierbeck (779–780) carried on similar studies and stated that evaporation should be measured.

Wolpert (986–989) studied the effect of moisture on laborers, the effect of oiling the skin on water loss, the influences of evaporation upon the skin, and the influence of air movement upon water loss and carbon dioxide production, confirming the results of others and adding further details. Up to 25°C., CO_2 production is increased by air movements; at higher temperatures, decreased. Haldane (362) worked upon the effect of high temperatures on man and found that the discomfort was due to a *rise of body temperature.* The ill-effects were partially prevented if the air was kept moving, thus increasing the evaporation.

Hill (401) summarizes the important work on the subject of water relations and heat regulation and adds the results of his own investigations. The heat regulating power of a mouse fails below 20°C. in a saturated atmosphere, due to rapid loss of heat, and the animal dies from cooling.[1] In man it fails at 29°C. in a saturated atmosphere and if he is active and clothed, he suffers from over-heating. At 37° and in the absence of clothing, any exertion is practically impossible. In a dry air a man may sit for a time at 100°C. Sutton also states that heat stroke occurs only in a very moist atmosphere (see 808). Aron (38), working on men and monkeys, found that death from exposure to the tropical sun in the Philippines was not due to any effect of the tropical light, as had commonly been supposed, but to an overheating of the body. This could be prevented by shade or by air currents which increased the evaporation. In conclusion he states: "My experiments demonstrate the enormous physiological and hygienic importance of ample water evaporation in the tropics."

All animals produce some water through the oxidation of the hydrogen in their food. A man produces about one-third to one-fourth of the amount of water which he gives off through the skin and lungs. Mathews called attention to this fact in connection with the adaptation of reptiles to desert conditions. Berger (77) studied the water relations of the meal worm (*Tenebrio molitor*) when kept in dry air and fed on bran which had been dried at 105°C. He

[1] These results are partially in error, as a repetition of the experiments indicates that lack of food may have been important.

considered that the animals were in essentially absolute dryness. Here they lived for weeks but lost weight. He found, however, that the per cent of water in the animals remained practically the same until after death and came to the conclusion that the insect larvae could not use their food to produce water and so the living substance itself was used. No doubt the food taken produced water, but this was insufficient in quantity. The most important fact brought out was that the per cent of water remained about the same in spite of the extreme dryness and rapid loss of moisture. Pernice and Scagliosi (666) worked upon fowls which had died of water starvation. They came to the conclusion that the possible water fluctuation of the animal tissues is very small and whenever a cell's water content passes a certain limit, death ensues. Hill (401) states that with a loss of ten per cent of his weight in water, a man usually dies.

Many animals, such as reptiles, which are abundant in deserts possess thick skins which prevent the loss of water by evaporation. Others, such as reptiles and birds, lose very little water in the form of nitrogenous waste, such waste materials being cast from the body in a nearly dry state. No mechanism to prevent loss of water exists in the common frog; its water demand is supplied through the skin. The common European frog died if the loss of water was rapid when 15 per cent of the frog's weight was withdrawn. If the drying was slow the frogs could lose 30 to 39 per cent of their weight in water without dying. When the weight was reduced to 61 per cent the blood corpuscle count was increased to two and one-half times the normal (808).

b. General summary of relations to evaporation and the reasons for its determination. On the basis of the experimental work cited, the reasons for the necessity of determining evaporation in connection with the effects of temperature, moisture, wind movement, and insolation may be summarized as follows:

(1) The total effect of air temperature, pressure, relative humidity, and average wind velocity upon a free water surface is expressed by the amount of water evaporated.

(2) The same factors have been shown to determine the amount of evaporation from the bodies of organisms (Reinhard 726).

(3) Metabolism results in heat and the temperature of the bodies of animals, both warm and cold blooded, is nearly always higher than the surrounding medium, at least during activity. The surrounding

conditions may be stated as usually acting on metabolism, etc., as follows: (a) A moist cold atmosphere (very low evaporation) causes body temperature to fall more rapidly than a dry cold one at the same temperature because of the more rapid conduction of heat. Such a fall in temperature *decreases* metabolism of *cold blooded* animals and *increases* metabolism of *warm blooded* animals within their capacity for heat regulation. In a dry cold atmosphere the heat loss is less pronounced because of the less rapid conduction of heat. (b) In a dry warm atmosphere (high evaporation) rapid evaporation keeps down the peripheral temperature, and prevents death from overheating and destructive metabolism in cold blooded animals, and makes possible body temperature regulation and thus prevents heat stroke and death in warm blooded animals. In a moist warm atmosphere, death and heat stroke occur because of lack of evaporation and lack of peripheral cooling in the case of warm blooded animals, even when the surrounding temperature is at or below the normal body temperature. (c) Wind movement (which increases evaporation) increases the loss of body heat and of heat due to insolation. It increases evaporation and thus further cools the body, increasing the metabolism of warm blooded animals and decreasing it in cold blooded animals. (d) Decreased pressure increases evaporation and radiation, both of which lower the temperature of animal bodies and influence metabolism, as stated under (c).

(4) Conditions which withdraw water from organisms (evaporation as influenced by various factors) influence irritability, activity, and length of life history. Thus Hennings found that low humidity increased insect metabolism and Sanderson found that in dry air the optimum temperature of the growth of insects was lower than in moist air. Thus there are no doubt many exceptions to the usual rules as given under (3).

The work summarized above shows that there is an excellent experimental basis for a statement of the factors controlling the distribution of animals. It is evident that *temperature* data have little significance unless the humidity is known. Neither of these can be interpreted without a knowledge of the pressure, insolation and wind movement. The experimental foundation for the consideration of all these factors in combination, in terms of evaporation, was laid down by Reinhard (726) and Rubner (753). The similarity of reaction and survival time of animals when exposed to air of

similar rates of evaporation regardless of whether due to *dryness*, *heat* or *velocity* speaks for the measure of evaporation. It is however evident that while these facts indicate importance of evaporation, it is an index of reactions and distribution and general success over long periods but is not, as will be shown, a good index of rate of development.

4. Effect on rate of development

There is not much correlation between the amount of evaporation and the rate of development of insects (Lathrop, (511)). This is probably due to the fact that the factors controlling evaporation act in opposite ways; thus, high humidity often increases the rate of development and lowers evaporation, while high temperature increases evaporation and increases rate of development. The writer (826) found no definite relation between the rate of development of the codling moth pupa and the evaporation rate.

5. General well-being

The correlations of distribution and general well-being with rates of evaporation are to be sought along the lines pointed out by Transeau (906), Livingston (520, 521, 525) and others.

III. MEASUREMENT OF EVAPORATION

Various methods of measuring evaporation have been used, especially in forest studies. The following statements concerning the field use of the various instruments are taken in large part, from Bates and Zon (66).

1. Porous cup atmometer (66)

The name "atmometer," while describing any instrument for the measurement of evaporation from a moist surface, is usually associated with evaporimeters of the porous cup type. A very satisfactory field instrument of this type, described in several papers by Livingston (520), may be obtained on the market either with or without standardization. Only standardized instruments should be used in comparative studies.

The instrument consists of a closed cup with porous walls, into which the water is drawn by the capillary action of the cup. Evaporation is determined by measuring the amount of water required to fill the flask to its original level. The use of a large flask so increases

the possibilities of the instrument for long-period observations that it is, in this respect, far superior to the Piche evaporimeter (761).

The moisture of the cup reaches the outer surface through the porous walls, its rate of movement being determined by the difference in capillary tension caused by the loss at the outer ends of the pores. Presumably capillary movement is sufficiently rapid to maintain the supply at the outer surface at any reasonable rate of evaporation. Yet there must be a limit to this capillary action in both directions, and for this reason the movement must, under extreme conditions, be governed somewhat according to atmospheric conditions by regulating the hydrostatic pressure. With the outside walls of the cup always moist and yet not dripping, the rate of evaporation will of course be governed by atmospheric conditions. It must not be expected, however, that the evaporation from this instrument may be compared under a variety of conditions with that from the Piche instrument, or with that from a free-water surface. While the absorption of heat from radiant sources and conduction from the air will be practically the same for the water surfaces in the three cases mentioned, yet the further absorption beyond the first water surface will depend on the nature of the substance behind that water surface—in the one case, water; in the second, paper and glass; in the third, clay or some similar earthy substance. Therefore, the three instruments will respond quite differently to the stimuli of warm air and sunshine.

For these reasons, comparative data will be of value only when the same instrument is used in all measurements of the comparison.

In 1910, Livingston described a rain-correcting atmometer. This atmometer, while giving great satisfaction in the hands of many inexperienced workers, was difficult to operate in some localities. Thus it was found impossible to obtain continuous records in the dry climate of the Wasatch Mountains of the Manti National Forest in central Utah, principally on account of the connections and joints of the equipment, all of which occurred outside of the water reservoir. Hail storms and objects carried by strong wind were often so severe as to disjoint or break the more delicate equipment. In connection with this instrument, it is understood that the automatic mercury valves which operate to prevent the water absorbed by the porous cup in times of rain from entering the reservoir are externally situated. This makes it essential to have all valves very tightly connected in order to prevent leakage.

The Livingston porous cup atmometer measures the evaporating power of the air with a very considerable degree of accuracy during periods when the temperature is not at or below zero centigrade.

2. Measurement under experimental conditions

The writer investigated the relation of air movement to evaporation. The results are shown in table 29. Because of its relation to air

movement, evaporation should accordingly be measured, not only on account of its importance in connection with measured temperature and humidity, but also on account of the fact that rate of air movement is not necessarily otherwise measurable in terms which have bearing on the life processes of organisms.

The Livingston porous cup atmometer was generally used in the writer's experimental work and was commonly merely inserted in the cage where animals were confined. One difficulty that has to be avoided is having the atmometer too near the animals or in such a

TABLE 29

Showing the relation of evaporation to air velocity and to relative humidity under experimental conditions, together with the relative rate of increase of evaporation and velocity (0.52 meter per second equals 1.1 miles per hour, 0.68 equals 1.5; 0.10 equals 0.2). The equipment is not accurate enough to make this more than a general guide. Pressure was not read

APPROXIMATE VELOCITY PER SECOND	APPROXIMATE EVAPORATION PER HOUR	TEMPERATURE	RELATIVE HUMIDITY IN PER CENT OF SATURATION	RATIO: Increase in flow	RATIO: Increase in evaporation
meters	*cc.*	*°C.*			
0.012	0.25	22.4	50	1	1.0
0.026	0.40	22.2	53	2	1.6
0.052	0.75	22.2	53	4	3.0
0.104	1.50	22.2	53	8	6.0
0.208	2.00	22.2	54	16	8.0
0.416	2.60	22.2	53	32	10.4

position that they can come in contact with it, especially if the animals are inclined to contaminate the surface, as mice might do. One reason for keeping the atmometer at a distance from the animals lies in the fact that the temperature may be 1° or 2°C. lower in the immediate vicinity of the atmometer than in the cage generally. This has to be taken into consideration in the designing of cages for use of insects. It is necessary to construct the air inlet in such a way that the atmometer occupies the same position and gets the same air movement as the plant on which the animals live. This may be accomplished by designing the cages along the line of figure 178, page 421. For animals that may be contained in small bottles, it is necessary to pass the ventilating air first through the bottle and then over the atmometer through a space with the

same cross-section area. For animals like codling moth larvae, a central wooden dummy on which the moths are allowed to spin their cocoons and which is the same size as the atmometer may be used as shown in figure 131. Here the air entered the bottle containing the larvae, flowed over the animals under experimental conditions and passed out through another container of exactly the same size and over the atmometer. The second container may be

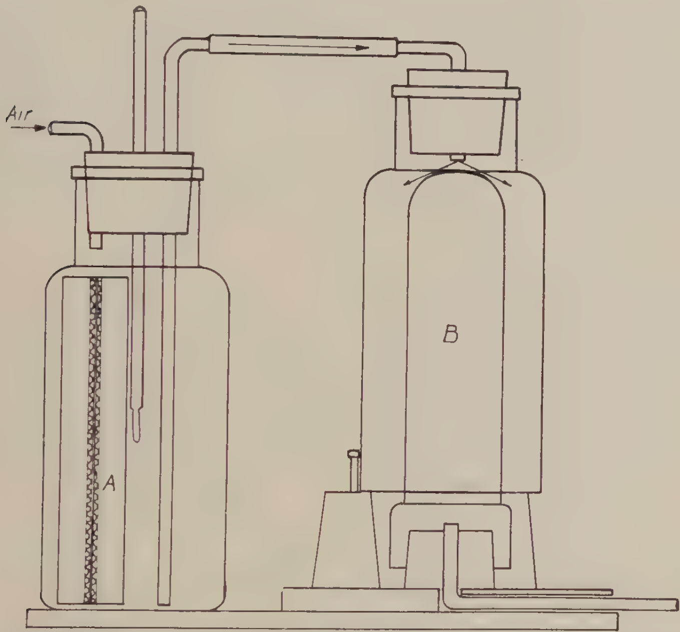


FIG. 131. An arrangement of two bottles used in measuring rate of evaporation in codling moth pupae experiments. *A* shows two pieces of wood with pupae in corrugated paper between them. *B* is the atmometer in a bottomless bottle of the same size and with the same free space as that surrounding A.

especially constructed of tin. The atmometers and larvae-holding dummies were arranged under the center of the inlet in the same position, so that the conditions of the withdrawal of water from the bodies of the larvae were essentially the same as from the atmometer.

Some experiments were performed by less accurate means. The size of two wooden containers which were tied face to face was the same as that of the atmometer, but the blocks were dropped into the experimental bottle so as to leave any inequalities in the rate of

evaporation to be corrected by the chance turnings and slight differences in position of the sticks from day to day. Whenever it is desired to measure the evaporation by passing air over an atmometer at the same rate as it passed through a chamber in which animals were observed, it is necessary to construct a device as shown in figure 131, of such size that the air passes through the free space with the atmometer in position at the same rate that it passed through the container in which the animals were kept.

Porous cup atmometers do not retain their standardization and should be changed and restandardized approximately once a month. The change of the rate of evaporation from the same atmometer is due to the solution of the wall of the cup which renders it more

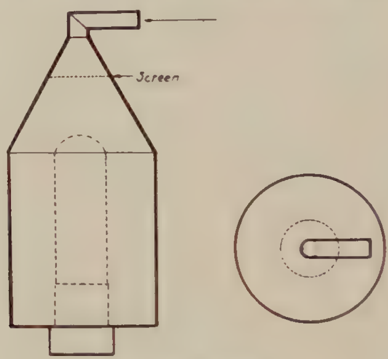


FIG. 132. A hood to serve the same purpose as the bottomless bottle shown in figure 131.

porous in some cases, in others to the fouling of the outside of the cup by oil and dust from the air that is used. To standardize the cups, they are rotated on a turn table together with a new cup of known standardization which is used for reference, and new standards are calculated from the evaporation of the known and unknown cups.

3. Continuous recording

Continuous recording of evaporation with the porous cup atmometer is now practicable through the work of Chalkey and Livingston (153a, *1929*), who have ingeniously restricted the flow of water

into the cup so that the reduction of pressure changes the level of mercury in a manometer attached to the cup. A float on the manometer operates the short arm of a lever which carries a pen in contact with a revolving drum, thus giving a record of rate. There is a filter paper atmometer manufactured by Jules Richard, Paris, but it cannot be standardized to agree with a porous cup atmometer. It is easy to construct recording devices for Livingston atmometers. One of these was described by Livingston at the 1905 New York meeting of the Botanical Society. This one made a mark on a drum whenever a definite amount of water was used. Another was reported by Sayre (776). One difficulty lies in the fact that the cups must be standardized, and the recording device has to be based upon the amount of the water actually used.

Black and white spherical atmometers have been used to determine the effect of light, or rather as a means of measuring light.

4. *Standardization of the porous cup atmometer*

The calculation of the coefficient of standardization has been explained by Livingston (520). It is three-fourths of the average loss from four pans, each exposing 60.10 sq. cm. of water, and this is treated as the reading of the standard cup.

Thus, if the pans lose in twenty-four hours $P1$, $P2$, $P3$, $P4$ grams of water, respectively, and the cup to be tested lost L cc., the coefficient for that cup would be

$$C = \tfrac{3}{4} \times \tfrac{1}{4} \cdot \frac{L}{(P_1,\ P_2,\ P_3,\ P_4)}$$

This coefficient is expressed in two places of decimals and is the number by which the reading of the cup must be multiplied to give the reading of the standard cup.

If the atmometers are standardized against another cup the formula would be changed to

$$C = \frac{Y \times P}{L}$$

Where Y equals the coefficient of the cup with the known standardization, and P the reading of that cup, L equals the reading of the cup being tested.

Cups should be left with water in them for some time before setting up, then run for an hour, examined for bubbles, and finally run for twenty minutes before starting the test.

If the original coefficient of standardization for a given cup be c and the coefficient obtained after four weeks' operation be c' and $c-c'$ is not more than 0.10, then the corrected reading, E, for each week is obtained by multiplying the actual reading, R, by

$$\frac{c+c'}{2} \text{ or } E = - R \cdot \frac{c-c'}{2}.$$

When $c-c'$ is greater than 0.10, we may correct for the first week by the following formula

$$E = R\left(c + \frac{(c-c')}{N}\right),$$

and for the third week by

$$E = R\left(c + 3\,\frac{(c-c')}{N}\right), \text{ etc.}$$

where N is equal to the total number of weeks that the atmometer ran. The numerical coefficient of the fraction (3, above) is the serial number of the particular week in consideration.

5. *Forest Service evaporimeter* (*Bates and Zon* (66))

To fill the need, in forest studies, for a substantial, essentially indestructible evaporimeter, operating as well in winter as in summer (since it can not be conceded that biological activity ceases with the first occurrence of frost), Bates (65) has designed a metallic, "inner cell" evaporimeter. In addition to these desired practical qualities, it was conceived that an evaporimeter might more closely resemble the leaf, and thereby might show a closer correlation with plant transpiration, by having the evaporating body somewhat protected from air currents. Evaporation takes place in the leaf, not largely on its surface; and, while transpiration is accelerated by wind movement, the latter can not have the direct action upon the water in the leaf and its formation into vapor that it has upon a fully exposed surface.

The correctness of this principle has been demonstrated by comparative tests of evaporation and transpiration under a variety of conditions. The evaporimeter may be briefly described as follows:

The tank or reservoir has a capacity of about 450 cc. sufficient for a week's

operation under extreme conditions. It is seamless and is not ordinarily injured by freezing. It is protected by an outer shell of polished metal, which insulates it both against temperature changes and against direct radiation.

Out of the tank rises a stem a few inches long and one-half inch in diameter, carrying the feed-wick, which is a piece of linen rolled into cylindrical form with the threads "drawn" at one end. At the top of the stem this wick is flattened out to make a contact with the evaporating wick. The evaporating wick is a flat, circular piece of linen having an area of 100 sq. cm. It rests upon a perforated metal disk of the same size, the perforations aggregating an area of 5 sq. cm., and designed to simulate the stomata of the under side of a leaf. All vapor formed must escape through these perforations. The disk is firmly attached to, and flush with, the upper end of the stem.

Over the wick is a cover only slightly larger than the disk, whose flanged edge extends down over the edge of the disk. This is held down by two screws, which engage the flanged edge. The cover is flat, but seamless, and completely excludes rain or snow. Its surface is finished with nickel and an instrument having this polished surface absorbs practically no radiant energy and is called a "shade" instrument. To obtain the effects of radiation, an instrument whose cover has been coated dead-black is used. The "shade" instrument is now entirely abandoned, since it has been seen that the difference between the two is not a measure of sunlight intensity, but a measure of the additional effect of sunlight in producing evaporation. This effect can not under any circumstances be ignored in ecological studies.

The tests which have been made show that the losses from the blackened instrument of this type follow more closely those from potted trees, under a great variety of atmospheric and solar conditions, than do the losses from any other type of instrument at present available. The instrument has also shown itself remarkably free from annoying characters, and responsive to all degrees of evaporation stress. It may be considered, however, something of a disadvantage that the amount evaporated is relatively small. The losses for short periods may, therefore, only be determined by very precise weighing.

6. *Piche evaporimeter* (*Bates and Zon* (*66*))

The Piche evaporimeter, as modified by the Weather Bureau, was used considerably 10 years ago and has been described by Russell (761). It consists of a graduated glass tube as a reservoir for the water and a filter paper held over the open end of this tube by means of a horizontal glass plate, a spring, and a pressure screw. It is commonly equipped with a 10-cm. (4-inch) glass plate and a 9-cm. filter paper under ordinary conditions, or a 5.5 cm. paper of the same make when evaporation is likely, between observations, to exceed the capacity of the tube, about 40 cc. The larger paper exposes 60.91 sq. cm. and the smaller 21.06 cm. Therefore, quantities evaporated from the smaller papers should be multiplied by 2.891 to make them approximately comparable with the others.

Distilled water should be used in evaporimeters, both because of the effect

of soluble substances and to keep the instruments clean and free acting. A nonfreezing solution (66) of 25 per cent denatured alcohol and 75 per cent distilled water has sometimes been used in cold weather; but the value of records obtained under such conditions is questionable, because at times the evaporation is almost wholly from the alcohol, and the ratio between alcohol and water or ice would, of course, depend very largely on the temperature. For this reason the instrument can not properly be considered for freezing weather.

The regulation of pressure on the glass plate is a somewhat complicating and bothersome factor. In dry weather the pressure must be made light to feed the paper sufficiently, and in damp weather it must be quite firm to prevent overflowing on to the glass, if not actual dripping.

Evaporimeters of this kind may best be suspended on wires, having hooks at their lower ends, so that the instruments may be readily taken down for filling. In filling, a long 50-cc. pipette is found most convenient, making it possible to keep the outside of the tube dry. Care should be taken to have the filter paper wetted and adhering closely to the glass before the instrument is read and left.

It is unnecessary to calibrate these instruments, because of the frequent changing of the filter papers and the fact that papers of one grade may be quite uniform in their capillary properties. Beyond this, the evaporation rate is somewhat controlled by the adjustment and the degree to which the paper is wetted.

The Piche evaporimeter is not now considered so desirable an instrument as some of the other types. Though it is simple and fairly easy to operate under most circumstances, it is fragile and hardly suited to severe weather conditions; the adjustment of the feeding for changes in the weather is always vexatious and sometimes beyond one's power; a correction for rainfall is out of the question; and the technical point may be raised that the moist surface is somewhat too freely exposed to wind, while the white filter paper absorbs only a small proportion of incident radiation. The conditions for evaporation are, therefore, very different from those within the leaf.

7. General suggestions (66)

With the Bates Forest Service evaporimeter, the daily observations consist in weighing the instrument, usually on an inexpensive balance. Refilling is undertaken as often as necessary to maintain between 100 and 200 cc. of water in the tank. The "closing" weight and "refilled" weight are recorded together with the number of the instrument.

In the case of the Piche evaporimeter, losses are calculated from the readings of the graduated reservoir. Note should always be made of observed overflowing or drying-up of the filter paper or evaporating surface and the probable correction due to these failures of the instrument should in all cases be estimated.

IV. EXPERIMENTAL CONTROL OF EVAPORATION AND PRESSURE

The works of Bert, Cohnheim, Haldane and others supply suggestions as to equipment for large animals. The use of apparatus designed to control drying operations in industry, makes possible the control of pressure with continuous recording of conditions while the air is being changed at a fairly rapid rate. The principles used are similar to those employed in temperature control. The cam mechanism (page 223) may be used for a pressure program for the day.

1. Evaporation (378)

Evaporation at constant temperatures and humidities may usually be varied by changing the rate of air movement (10). This is the only method employed by the writer. The flows were set with the diaphragm chamber daily and the evaporation determined by the use of Livingston atmometers. This method of increasing evaporation is less likely to change other factors than differences in pressures.

TABLE 30

Relation of size of U-tube to pressure or vacuum secured before air is passed

DIAMETER OF U-TUBE	HEIGHT OF MERCURY IN U-TUBE	MERCURY IN MANOMETER	
		Pressure	Suction
mm.	*mm.*	*cm.*	*cm.*
22.5	85.0	14.25	12.75
20.0	77.0	12.25	11.25
14.0	40.0	6.25	5.50

2. Pressure

Pressure has direct effects on evaporation. In climate simulation it is not necessary to exceed 800 mm. or decrease to less than 300 mm. of mercury.

In small containers, reduced pressure may be accomplished by a U-tube and mercury column. Air is drawn into the chamber from the short to the long arm of the tube. As soon as the air is pushed past the center of the tube, bubbles slip by the mercury column and the container is ventilated at a low pressure. Increased pressure may be accomplished by attaching the same U-tube on the outlet

and ventilating with compressed air. The rate of ventilation must be very slow to prevent mercury loss. Ordinarily not more than 25 cc. of air per second can be passed by mercury with an ordinary straight tube. The larger the tube within ordinary limits the greater the pressure or vacuum secured before air is passed. Table 30 shows this relation. A spherical bulb in the long arm of the U-tube is important for safety.

The same principle is illustrated by figure 210 (page 515) and its application by figure 211 (page 516). The apparatus shown in figure 210, when used for reduced pressure, has the mercury valve on the exhaust side. Air is admitted through a very small opening. In the apparatus just mentioned, the air is admitted through a large U-tube in the position of the manometer, which eliminates the necessity of adjusting a slow leak. The cylinder shown in figure 210 could doubtless be used in the same way.

CHAPTER XIII

Light Conditions and Effects

I. INTRODUCTION

The effect of light upon organisms was receiving considerable attention about 1890, but after the methods and apparatus available for its control at that time had been exhausted, attention was turned to other fields, and the physiological effects of light received little attention for about twenty-five years. The discovery of ultraviolet effects, together with the development of various artificial lights and the improvement of photometric methods, has led to a re-investigation of the subject. Results thus far obtained indicate that the control of light can no longer be neglected in climate simulation. The study of its physiological effects is a promising field generally.

TABLE 31

Relative illumination intensities, from the Smithsonian Meteorological and Physical Tables (1918) (852)

	M.C.	F.C.
Zenithal sunlight	103,324.0	9,600.0
Sky at end of civil twilight	355.0	33.0
Sky at sunset	4.30	0.40
Zenithal full moon	0.211	0.02
Starlight*	0.00086	0.00008
Minimum light visible to eye at 1855 meters distance	5.00	0.47

* The eye can distinguish stars the light from which is about 0.000,000,000,-00,1 of full sunlight (or full sunlight $\times 10^{-13}$).

II. LIGHT CONDITIONS IN NATURE

A brief synopsis indicates that the amount of light (intensity), when all wave lengths are present, influences the growth of animals, and that the quality of the light (wave-lengths present), the direction of the rays, and change and periodicity of intensity also have important effects.

1. Light conditions in natural habitats

Intensity of sunlight. Table 31, taken chiefly from the Smithsonian tables, (852) shows relative intensity of sunlight and other lights.

2. Light at different altitudes, latitudes, and hours of the day

a. Atmospheric path and transmission (2, 3, 4, 5). Figure 133 shows the relative energy in sunlight between 300 and 1,600 mμ (from Abbot and Fowle (3), curves to 1800 omitted), first for the sun's radiation outside the earth's atmosphere (curve *o*) and for radiation through various atmospheric paths. The atmosphere is commonly referred to as an air mass for locations near to sea level so that the figures, as given in the broken curves numbered *1a*, *2a*, etc., are for the sun's radiation through a number of air masses which varies with latitude and the hour of the day. More recent figures are similar (fig. *B*) (259, 471). The maximum energy of sunlight shifts from 470 to 700 mμ, depending upon the number of air masses through which the radiation passes. The energy in the extreme violet drops off very rapidly, beginning in the vicinity of 400 mμ. The reason for this is evident from a comparison of the transmission coefficients for the different wave lengths. Table 34 shows the transmission coefficients for the sun's radiation or energy through one atmosphere or one air mass, so that from these coefficients energy curves may be constructed for any number of air masses by computation from the curve in figure *A*, which is designed to show the

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FIG. 133. *A*. Showing the effect of atmospheric path and altitude on the intensity of solar radiation. The average normal energy curve of the solar radiation outside the atmosphere (line 0), the average normal energy curves at Mount Wilson (altitude 1789 meters) and at Washington, numbered 1a, 2a, 3a, 4a and 6a and corresponding to air masses 1, 2, 3, 4, and 6 which occur with the sun at the approximate zenith distances of 0°, 60°, 70°, 75°, 80°, respectively. The Mount Wilson determinations are given in full lines and the Washington ones in dotted lines (3). And the Mt. Wilson numbers are secants through the reduced atmosphere.

B. Curves of relative intensity of solar radiation after Kimball (471).

0. Outside the earth's atmosphere.

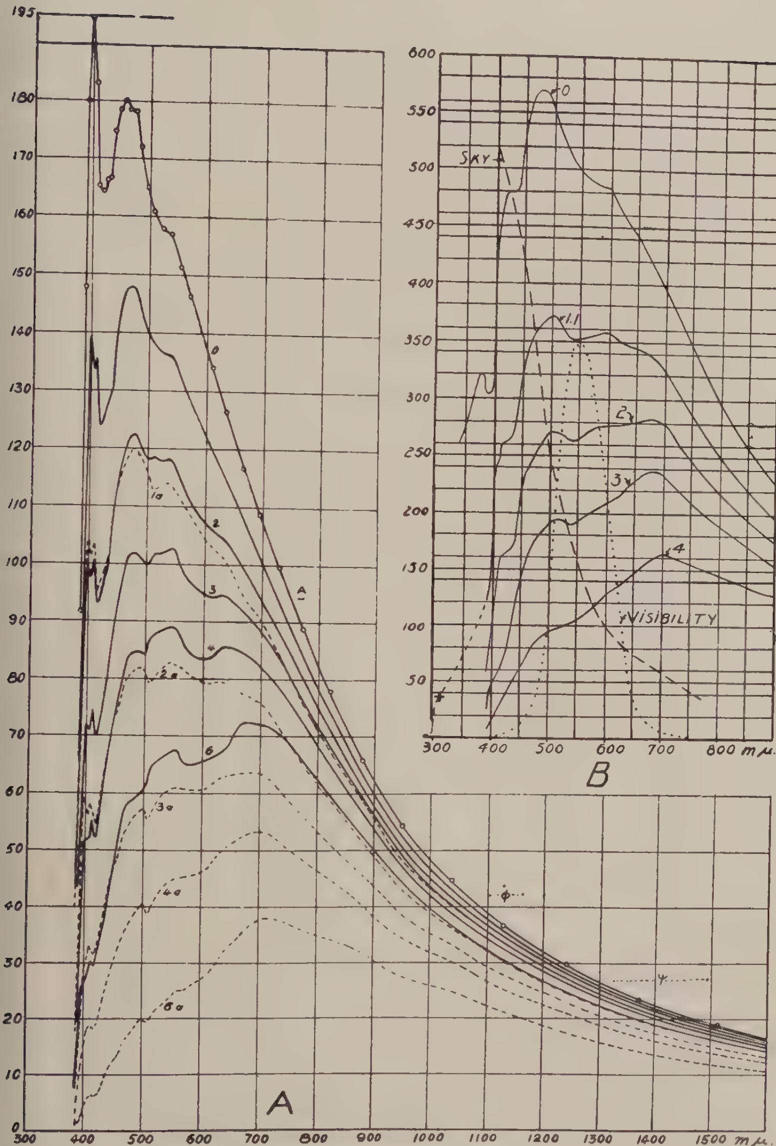
1. At Washington with a zenith distance of 25° (1.1 air masses). The broken line at the left shows an approximate distribution of ultraviolet, the small *x* is on 320 and was obtained by multiplying the energy value for this wave length by .32 which is Dobson's (251) largest coefficient for 1922.

2. The same as 1, Zenith distance 60° (2 air masses).

3. The same as 1, Zenith distance 70.7 (3 air masses).

4. The same as 1, Zenith distance 78.7 (4 air masses).

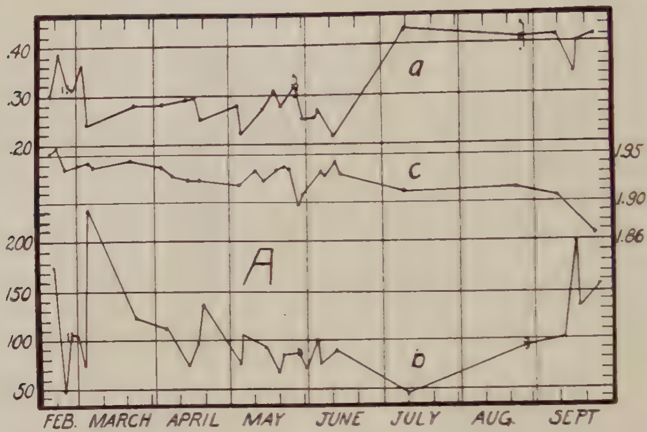
The sky intensity on Mount Wilson is shown by a dash line.



NORMAL SPECTRUM ENERGY CURVES

FIG. 133

distribution of the sun's energy outside the earth's atmosphere. For example, if the mean zenith distance between 9:00 a.m. and 3:00 p.m. for a given locality and season is found to be such that the



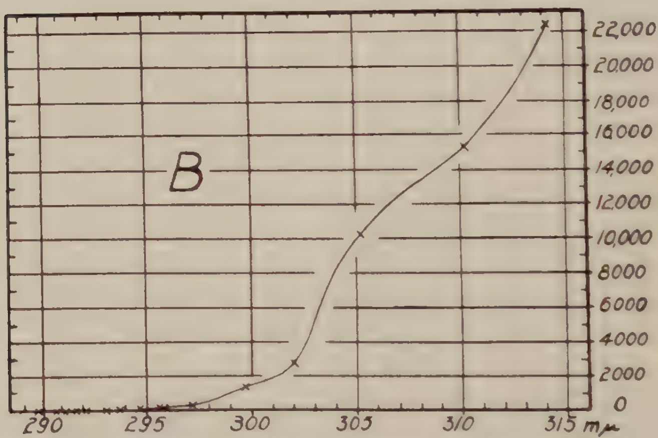


FIG. 134. *A*. *a*. Variation in the transmission coefficient for radiation of wave length of 315 to 320 mμ at Oxford, in 1922 (251).
b. Variation in intensity of the same.
c. Variation in the solar constant (Washington).
B. The relative intensity of ultraviolet at the earth surface (with sun at zenith) Marseilles, France, June 7, 1922. (286) (see table 33).

sun's path is increased to 1.13, then the energy curve may be derived by raising each of the coefficients to the 1.13 power. Figure 133*B*

hows the sun's energy by wave-lengths after Kimball (471) and ltraviolet according to Fabry and Buisson (286). Figure 134, *A*, hows variations in ultraviolet intensity from day to day. On the .1 air mass curve in figure 133*B*, Dobson's datum (from fig. 134) or 320 mμ is shown by a cross and the curve extended to 290 mμ. 'riest (702) offers further data. The transmission of ultraviolet by

TABLE 32

Variations of the limits of ultraviolet

TIME OF DAY AND LIMIT IN mμ (ACCORDING TO CORNU AFTER LUCKIESH)		ALTITUDE AND LIMIT IN mμ (ACCORDING TO MIETHE AND LEHMANN AFTER LUCKIESH)	
10:30 a.m.	295.5	50 M.	291.26
12:02 p.m.	295.0	116 M.	291.55
1:18 p.m.	295.5	1620 M.	291.36
1:50 p.m.	297.0	3136 M.	291.10
3:09 p.m.	299.0	4560 M.	291.21
3:40 p.m.	304.5		
4:17 p.m.	304.5		
4:38 p.m.	307.0		

TABLE 33

elative energy in the sun's ultraviolet at the earth's surface June, 1920, Marseilles, France (Fabry and Buisson (286))

WAVE LENGTH	RELATIVE ENERGY	WAVE LENGTH	RELATIVE ENERGY
314.3	22,400.00	293.6	11.00
310.4	15,100.00	293.1	5.50
305.2	10,200.00	292.2	2.20
302.2	2,700.00	291.7	0.87
299.7	1,320.00	291.2	0.30
296.3	132.00	290.6	0.04
295.6	76.00	289.8	0 02
294.6	25 00		

ie atmosphere is very important because of the important effects ' low intensities of these wave lengths (539). Wave lengths from)0 mμ, the limit of visibility, to 290 mμ the approximate limit for ie sun's radiation are called the near ultraviolet (these limits are ommonly put at 400 mμ to 300 mμ but in climatic work it is best use the limits of the sun's spectrum 290 mμ). Luckiesh (539) has scussed these limits and gives a summary of the literature. Dorno

(259) has also discussed it. Luckiesh also states that one observer found the limit for observations made with a photoelectric cell at an altitude of 4560 meters at 280 mμ. The intensity of radiation (286) at 290 mμ is only one millionth as great as at 315 mμ. From 315 to 290 radiant energy decreases very rapidly. Figure 134 shows

TABLE 34

Solar spectrum energy (arbitrary units) and its transmission by the earth's atmosphere (852)

Values computed from $e_m = e_o a^m$, where e_m is the intensity of solar energy after transmission through a mass of air m: m is unity when the sun is in the zenith, and approximately = second zenith distance for other positions; e_o = the energy which would have been observed had there been no absorbing atmosphere; a is the fractional amount observed when the sun is in the zenith.

WAVE LENGTH	TRANSMISSION COEFFICIENT*			
	Washington	Mount Wilson	Mount Whitney	One mile nearer earth
mμ				
300		(0.460)	(0.550)	
320		0.520	0.615	
340		0.580	0.692	
360		0.635	0.741	
380	(0.380)	0.676	0.784	0.562
400	0.560	0.729	0.809	0.768
460	0.690	0.832	0.887	0.829
500	0.733	0.862	0.919	0.850
600	0.779	0.900	0.940	0.866
700	0.858	0.950	0.964	0.903
800	0.886	0.970	0.976	0.915
1,000	0.922	0.980	0.975	0.941
1,500	0.938	0.976†	0.965	0.961
2,000	0.912	0.970†	0.932	0.940

* Transmission coefficients are for period when there was apparently no volcanic dust in the air.

† Possibly too high because of increased humidity towards noon.

the rapid decrease in ultraviolet beyond 305 mμ. The limit of ultraviolet varies with the hour as shown in table 32 but not with altitudes up to 4560 meters. The general conclusion from the observations summarized by Luckiesh is that the abrupt "cut off" to short wave length radiation is due to ozone in the upper atmosphere.

b. Daily march of sun intensity and sky effects. At sunrise the un's rays pass through more than nineteen air masses. This is educed to half in the first ten or fifteen minutes and to a sixth in the rst hour, after which it gradually falls to a minimum of one air

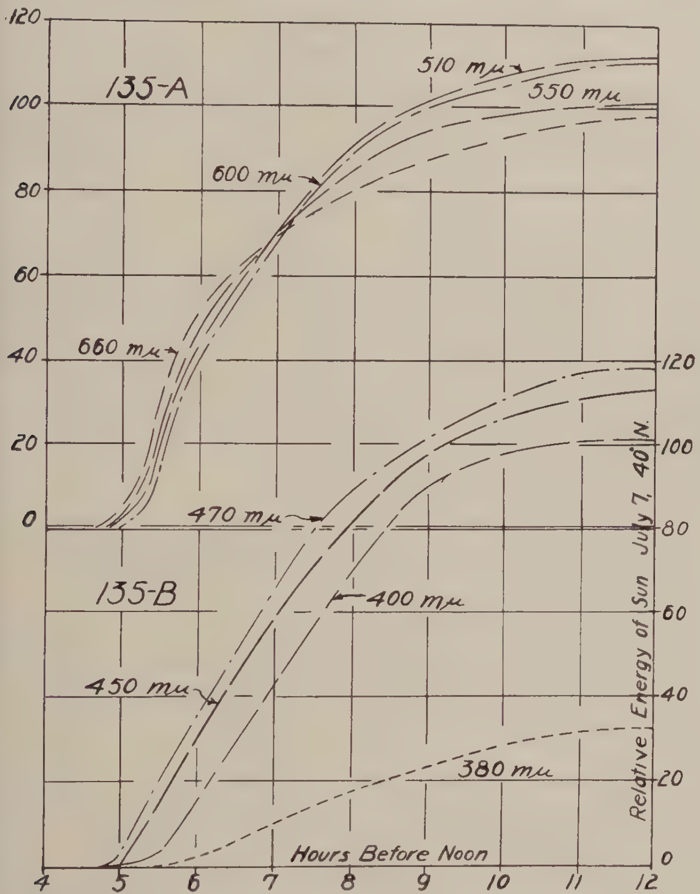


FIG. 135 *A* and *B*. Showing the forenoon march of light intensity at different ve lengths as calculated from air mass data taken from figure 133 A for ly 7, at 40° 7′ north latitude, Altitude, 225 m.; used as 40° N. and sea level.

ass or a little more at noon, depending on the season and latitude. e sky is an important factor in short wave length illumination ee skylight in figure 133, *B*). This factor enters into continuous

records of instruments, especially those of instruments sensitive to blue, making up a large part of the total blue and violet effect. Lord Rayleigh in his "Encyclopedia Britannica" account of the sky, states that under certain conditions half of the sky light may be polarized.

TABLE 35

Air masses

Besides values derived from the pure secant formula, the table contains those derived from various other more complex formulae, taking into account the curvature of the earth, refraction, etc. The most recent is that of Bemporad (852).

	ZENITH DISTANCE*								
	0°	20°	40°	60°	70°	75°	80°	85°	88°
Secant	1.00	1.064	1.305	2.000	2.924	3.864	5.76	11.47	28.7
Forbes	1.00	1.065	1.306	1.995	2.902	3.809	5.57	10.22	18.9
Bouguer	1.00	1.064	1.305	1.990	2.900	3.805	5.56	10.20	19.0
Laplace	1.00			1.993	2.899		5.56	10.20	18.8
Bemporad	1.00			1.995	2.904		5.60	10.39	19.8

*The Laplace and Bemporad values, Lindholm, Nova Acta R. Soc. Upsal., 3, 1913; the others, Radau's Actinometric, 1877.

TABLE 36

Showing relation at 49° north latitude

For foot candles, divide by 10.7584

MONTH	SUN'S ZENITH DISTANCE; NOON, 21ST OF MONTH	HOUR WITH CORRESPONDING ZENITH DISTANCE ON JUNE 21	RELATIVE INTENSITY IN METER CANDLES*
January	68.4	5:15 p.m.	65,174
February	59.0	4:30 p.m.	79,515
March	48.7	3:20 p.m.	89,359
April	36.5	2:00 p.m.	96,599
May	28.3	1:00 p.m.	99,472
June	25.5	Noon	100.429
July	28.0	1:00 p.m.	99,472
August	36.4	2:00 p.m.	96,599
September	48.0	3:20 p.m.	89,359
October	59.2	4:30 p.m.	79,515
November	68.5	5:15 p.m.	65,174
December	72.0	6:15 p.m.	58,202

* Based on wave length = 500 mμ.

When the sky is overcast the violet and blue are relatively more
tense than when it is clear, but the total light is small. Figure 135
iows the sun's intensity for different wave lengths without skylight,
calculated for Champaign, Illinois, July 7 from figure 133, *A*,
id the use of transmission coefficients.

c. Annual march of noon intensity. This is determined by the
mospheric path. At 49° north latitude, the relation of intensity
various hours is shown in table 36. Noon on December 21 has
ie same atmospheric path as 6:15 p.m. on June 21, which is nearly
ro hours before sunset.

d. Climatic data. Light is influenced by cloudiness, water vapor,
c. Each locality has its clearest and cloudiest months. There is,
cordingly, a direct relation between light conditions and weather
id climate (2, 168, 411). The total hours of sunshine per year,
onth, or day is an important part of meteorological records.

In addition to weather effects, there is the effect of vegetation
ver. Many animals never come into the light even though there
no vegetation in the habitat. Others, such as birds, may seek
ll sunlight above a forest of the most impenetrable character.
iese statements do not, ordinarily, apply to the dominant or
undant animals of the temperate region.

The forest crown or any other cover of vegetation is probably
lective as to wave lengths absorbed and transmitted. Weese
60) found the light on the forest floor in an elm-maple forest near
bana, Illinois, to be about 1/400 of full sunlight. Allee (15)
ınd 1/442 of sunlight in the Panama rain forest during the dry
ason. Allee and Weese both indicate a vertical gradient upward
om the forest floor, to higher intensities. In deciduous forests
ere is a great change when the leaves fall. The study of the
ective absorption light by vegetation cover, requires special
ıdy with spectrophotometric equipment or with electrometric
asuring instruments (see page 348). Figure 136, *A*, shows the
r cent of light coming through a dense cover of young conifers, and
6, *B*, shows the effect of a deciduous forest near Urbana, Illinois
00).

e. Reflection of light. Light including ultraviolet is reflected from
ves and flowers. Lutz studied flowers (541) and Shull (843),
ves (fig. 136*C*). Some ultraviolet is reflected from flowers and
visible to insects. The upper sides of leaves in diffuse light

reflect 3 to 6 per cent at 430 to 440 mμ; 4 to 9 per cent at 460 mμ; 4
to 10 per cent at 480 mμ; 4 to 12 per cent at 500 mμ; 5 to 16 per cent
at 520 mμ; 6 to 24 per cent at 540 mμ; 6 to 30 per cent at 560 mμ;

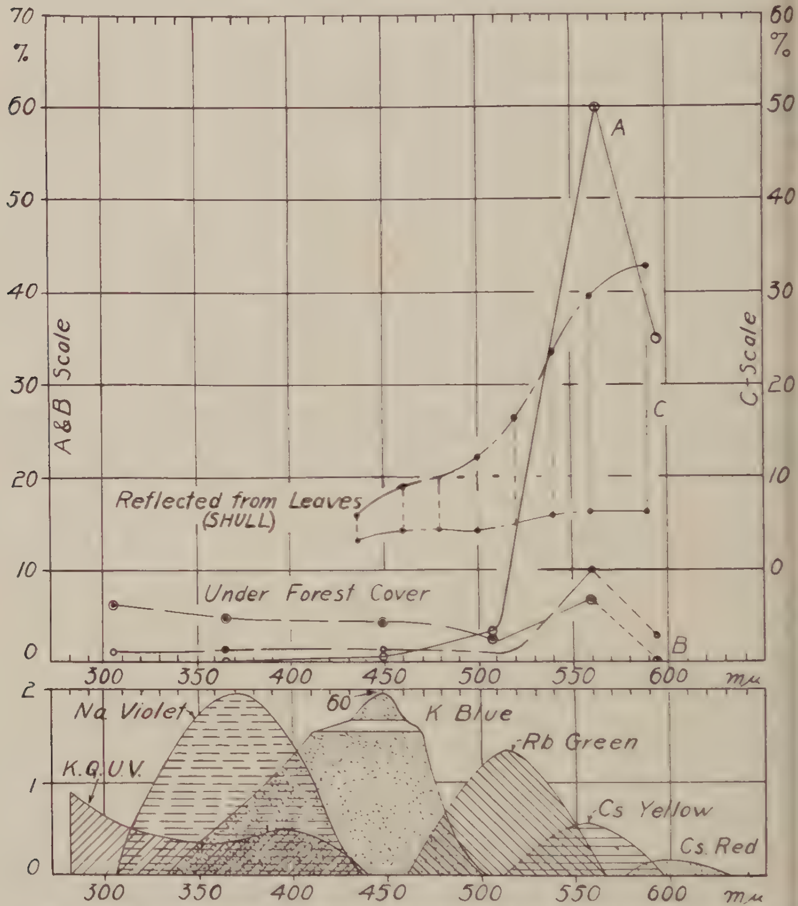


FIG. 136. A, B, C. The curves at the bottom show the sensitivity of th photoelectric cells and screens used on a wave length scale. Above, the pe cent readings for the different conditions are indicated in curves A and B above the maximum sensitivity of each radiometer; A shows the selectiv absorption of light by a dense cover of young conifers on San Juan Islan Washington. (832) B shows two series of readings for a deciduous fores at Urbana, Illinois. Above and using the right hand scale are shown th limits of reflection by leaves, from data by Shull (843). This figure suggest that apparent greater transmission at about 550 mμ may be due to reflectio

to 33 per cent at 580 mμ; etc. The maximum for normal green eaves is 540 to 560 mμ, decreasing again to 700 mμ. The autumn-olored leaves increase to about 680 mμ. The under sides of leaves eflect about twice as much light as the upper. Richtmyer (736) has tudied ultraviolet reflection (541).

f. Influence of angle of incidence. The angle of incidence is impor-ant and has been studied by Kimball and Hand (472). They give lata for surfaces facing in various directions, but more is given on he sky than sky and sun. Light intensity on vertical surfaces facing he sun falls off as noon is approached.

g. The sun's spectrum. The sun's spectrum is continuous but s marked by numerous absorption bands which weaken or eliminate ertain wave lengths. Such knowledge as we have of effects of pecific wave lengths leads to the belief that the bands may be of mportance in climatic effect, especially since they are not stable. Rowland's well-known work in this field and the instabilities dis-overed in the absorption bands may prove of value to biological nvestigation.

h. Variation in intensity—sunspots, etc. The report of the Mount Vilson observatory for 1926–1927 contains the following important tatement:

> The ratio of ultraviolet to green solar radiation, reduced to values outside he atmosphere, has shown considerable variation since June, 1924, although he change from day to day is small. With the value for June, 1924, as unity, maximum in the monthly means of 1.57 was reached in November, 1925; uring 1926 the ratio decreased to a low value of 1.28 in April, but then in-reased to 1.51 in February, 1927, and has varied between this value and 1.43 uring the first half of 1927. A considerable degree of correlation is found be-ween ultraviolet solar radiation, sun-spot numbers and the solar constant. The atmospheric disturbances seem to be nearly eliminated by the differential nethod employed, since the ratio of the values at the zenith to those outside he atmosphere remain practically constant.

III. LIGHT EFFECTS

A. On growth and general success

The problem of the effects of light on animals is very complicated, nd all methods must be considered with respect to these effects ather than from the standpoint of physics. Wave length must be ontrolled and measured. Intensity must be continuously recorded

under natural conditions and in experiments, and rigorously controlled in experiments. Direction of rays is important under certain conditions and cannot be neglected in studies of development. Changes of light intensity affect activity and must be fully investigated, in their relation to growth and development. (Yung (996–998); Davenport (236), bibliography and literature review.)

1. Effects of intensity and duration. Starving vertebrates lose weight more rapidly in the dark. Eggs of many animals are believed not to develop in light. The hen's egg is greatly retarded. Animals rarely lay eggs in light except when well protected by the shells or the like. Frogs lay eggs covered with a jelly in full sunlight. The results of Yung's (236) experiments on this subject are shown in table 37.

TABLE 37

Effect of light and darkness on the rate of development (236, 996 998)

	DAYS OLD	DARK		LIGHT	LIGHT DIVIDED BY DARK
			mm.	*mm.*	*per cent*
Lot I........................	30	Length	19.66	23.10	117
		Breadth	4 66	5 50	118
Lot I......	60	Length	30.30	32.16	106
		Breadth	7 16	7 66	107
Lot II.......................	25	Length	15.83	19 83	125
		Breadth	3 50	4 33	124

The eggs of snails (236) have been shown to hatch after twenty-seven days in light and thirty-three days in darkness. Iseley and Ackerman (428) state that light has important relations in the oviposition of the codling moth, the oviposition taking place when faint light is accompanied by optimal temperatures.

Clark (165) and later Laurens (512), in reviewing the literature from a medical viewpoint, called attention to a number of important principles involving duration and intensity.

(a) Certain chemicals, usually substances which are fluorescent, render microscopic animals sensitive to light. Hematoporphyrin has similar effects on mice. The effects are controllable by varying intensity and duration.

(b) Ultraviolet light in sub-lethal exposures renders Paramoecium sensitive to heat. It also inhibits fission.

(c) The red blood cells and haemoglobin in mammals are decreased after some time in the dark.

Murphy and others (165) also have shown that a five-minute exposure to sunlight, ultraviolet light, or heat, influences the number of lymphocytes. Dry heat increases their number. Ultraviolet stimulates lymphocytosis due to rays shorter than 300 mμ. Laurens adds further data.

(d) Clark (165) shows two tables and a graph bringing out the absorption of light by the skin, especially the large absorption of ultraviolet which is the cause of sunburn. Laurens calls attention to the rays transmitted by the eyes of different vertebrates. He also brings out the fact that the lens is the deciding factor for the eye and that the combined effects of all parts is usually to shut out still more of the short wave-lengths. The limit of transmission for the eyes of several mammals is as follows: Man, at 65 years old 419 mμ, at 4 years, 306 mμ; ox, 370 mμ; rabbit 374 mμ; horse 375 mμ; pig 352 mμ. Laurens also brings out the fact that some insects and crustaceans recognize ultraviolet. He also gives some detailed data on the penetration of various wave-lengths.

(e) Effects of light on metabolism. Laurens (512) states that, in spite of the general belief that light is beneficial, observation has indicated that men and animals can live in darkness for comparatively long periods of time without serious functional disturbances. He further believes that the idea that light increases metabolism is insufficiently supported by experimental data. He summarizes the literature in considerable detail. Judging from the effects of photoperiodism, most definite results are to be expected from alternations of periods of light and of darkness with variations in the intensity and duration of each.

(f) Photoperiodism (571, 582). Duration of exposure to light influences its effects. Garner and Allard (322), who first made use of the principle of "photoperiodism," were able to make ordinary fall-flowering plants blossom in summer or at any other season by the employment of a short day. Both plants and plant lice appear to respond to the same stimulus as far as sexual reproduction is concerned.

Marcovitch (571) found that the number of generative and pro-

ductive special forms can be controlled by length of day. The development of the sexes of several of the Aphididae under observation has been produced experimentally in early summer and appears to be governed by the length of day to which they are exposed, regardless of the temperature.

The normal appearance of the sexual forms of *Aphis forbesi* in Tennessee is in November. The exposure of strawberry plants bearing it to a short day of 7½ hours, beginning May 23, 1922, resulted in the production of both males and oviparous females in abundance by September 18. In 1923, strawberry plants were given the same exposure at about the time the eggs were hatching, starting February 23. The first oviparous females were observed on May 7, and the first eggs were laid May 22.

Conversely, under a long exposure, beginning September 4 out of doors, the sex forms of *Aphis forbesi* were inhibited from appearing and viviparous reproduction was still taking place when examined December 3.

The stimulus to migration of those plant lice having an alternate host was also found to be the relative length of day. By subjecting the secondary or summer hosts of several well-known migratory species, such as *Aphis rumicis*, *Aphis sorbi*, and *Capitophorus hippophaes* to short days of about 7½ hours, it was possible to produce the fall migrants and males in the latter part of May and early June. Oviparous females, of *A. rumicis* matured on snowball June 20, at the hottest time of the year, when the days are longest. The normal appearance of the sexes of these species is the latter part of October and November.

Ten generations of *Aphis sorbi* were produced on apple by June 12, with the possibility of many more, as the result of keeping the apple seedlings in the laboratory under subdued light and giving each generation a new plant. Winged forms appeared in each generation from the third to the tenth very sparingly, with no tendency to increase.

The length of day with relation to the time of hatching appears to be an important factor influencing the early or late production of migratory forms. Rowan (749) has suggested photoperiodic phenomena in birds and fishes.

Light is important in controlling daily activity of hens (412). By supplying henhouses with electric lights it has been found

possible to increase the length of the feeding period in winter, and thus increase the productivity of the hens. The effect of the light on the number of eggs produced is indirect (412). The artificial light gives the hens more time for eating. Rowan (749) has emphasized photoperiodism in connection with reproductive periodicity and migration.

2. Wave-lengths and effects (*color*). Unfortunately much of the work on colored light is not of great value, because of inadequate spectral analysis. However, the results are very suggestive and may prove on repetition to be acceptable at face value.

In 1905, Hertel (165) showed that different wave-lengths (with same energy) have different effects on Paramoecia.

Wave length in mμ	280	334	440
Time to death of Paramoecia in minutes	3	14	180

Sublethal doses cause heat sensitization and death at normal optimum temperature. The germicidal action of ultraviolet is mainly in the shorter wave-lengths below 296 mμ (Luckiesh (539), p. 210).

The disease known as rickets is primarily a failure of calcium deposition in growing bones. (Clark (165), bibliography and literature review.) This disease can be produced by feeding a diet deficient in phosphates; additional calcium in the diet has no helpful effects. According to Clark, Huldschinsky reported that the ultraviolet rays had curative action in rickets. Hess and Weinstock (394) demonstrated by radiographs that sunlight alone has the same effect as ultraviolet rays. This effect will not be produced if the light has to pass through ordinary glass or clothing. Hess found that exposing rats to sunlight had effect in preventing rickets as did addition of phosphates or cod liver oil to diet. Rickets is characterized by low inorganic phosphate content of blood. During light treatment phosphate is increased to the normal amount. These observations furnish the first definite evidence of metabolic change in animals brought about by solar rays. Luce (538) demonstrated in experiments carried on at the Thompson Institute that rays in sunlight shorter than 305 mμ prevent rickets.

Hoyles, Payne, and Latshaw (412) found that short exposures of hens to ultraviolet light prevented rickets and increased egg laying and hatchability of eggs. They used light from the sun or a quartz mercury lamp. Levy and Gassul (165) exposed mice to ultraviolet

light (wave-lengths not stated) and killed and examined them. In the lungs red corpuscles were in the alveoli, spleen and liver were engorged with blood; supposedly, the effects were at the surface and the substance formed stimulated the internal organs.

Chick and Roscoe (162) found that the amount of vitamin D (antirachitic vitamin) in milk was directly proportional to the

TABLE 38

Effect of colored light on tadpoles (measurements in mm.)

From Davenport after Yung (236, 699, 996–998)

	ONE MONTH UNDER LIGHT			TWO MONTHS
	Average length	Average breadth	Length compared with white light	Length compared with white light
White	24.43	5.37	100	100
Violet	28.58	6.75	117	134
Blue	25.66	5.70	105	107
Yellow	24.37	5.46	99	102
Red	20.37	4.66	83	86
Green	16.99	3.91	70	Dead

TABLE 39

Hatching of eggs in days (236)

SQUID (*Loligo vulgaria*)		TROUT (*Salmo trutta*)		SNAIL (*Lymnaea stagnalis*)		AVERAGE ORDER
	days		days		days	
Violet	50	Violet	32	Violet	17	Violet
Blue	53	Yellow	34	Blue	19	Blue
Yellow, Red	58	Blue, White	35	Yellow	25	Yellow
				White	27	White
Green	62*	Green	36	Red	36	Red
White	Died			Green	Died	Green

* None hatched.

exposure of the cow to the sun. Laurens (512) calls attention to confirming work with artificial light (fig. 50, p. 111).

Northrup (512) found that light intensity produces aging in darkness-bred flies (200 generations) of the genus Drosophila, thus shortening the span of life. The length of the period is decreased by lower intensities and increased by higher ones.

3. Results with ray filters. The older work on aquatic animals and that on silk worms is of interest, but there is little known as to intensity, and the quality is known only in a general way.

(a) Results on aquatic animals. The work of Yung as summarized by Davenport is very suggestive and well worth repeating with modern equipment and exact methods.

Green rays are supposed to retard growth. This is indicated in tables 38 and 39.

(b) Results on terrestrial animals. Davenport has summarized the literature covering some terrestrial animals. The size of fly larvae varies with the color of light. The figures in table 40 indicate relative size after equal exposures (236), (996–998).

The effect of light upon the silk-worm has been shown by studies in Japan by Tanabe, Sakurai, and others.[1] Although there is a con-

TABLE 40

Relative size of fly larvae after equal exposures (236)

	RED	ORANGE	YELLOW	GREEN	BLUE	VIOLET	WHITE
Flesh fly larvae	8	7	6	4	9*	10*	5

* Largest.

siderable amount of the data on the effect of light on the growth and vigor of the silk-worm, the results obtained by different investigators are by no means in good agreement. It is, therefore, not yet possible to draw a sound conclusion. According to Sakurai, the results of the experiments conducted by foreign investigators are nearly similar to those of the Japanese authors. We will consider briefly some of the results obtained by Japanese authors in experiments on the effect of light on the silk-worm.

In most of the experiments conducted in Japan, silk-worms were reared in cages, the four sides and the top of which were made of colored glass plates. The top of the cage was provided with a small hole and the bottom was constructed in such a way as to permit free movement of air. To give a weak illumination, glass plates painted

[1] Extracted from a summary prepared for the author by Dr. C. Harukawa the Ohara Institute.

black were used. The semi-darkness in such cages is certainly not the same as in the experiments by other authors.

Since glass plates were used to obtain light rays of different wave-lengths and different degrees of illumination by white light, exact light energy or light intensity was not known.

(1) Effect of light on growth and development. Whether the silk-worm is reared in the light or in the shadow, seems to have some effect on the rate of growth. Tanabe (874), Tazawa (887), Sakurai and Takemura (764).

Experiments on eggs and hatching seem to be very rarely done. Tazawa (887) stated that the egg of the silk-worm developed slightly earlier in the dark than in the light. Certain authors, however, do not agree with this opinion.

TABLE 41

*Number of sick silk-worms per 1000**

LIGHT	SHADOW	VIOLET	BLUE	YELLOW	RED
143	270	186	390	194	137

* After Kawara, J. (465).

(2) Effect of light on the vigor of the silk-worm. In every experiment here cited, a large number of silk-worms were reared together in a cage. When the silk-worm begins to "sleep," i.e., to prepare for moulting, the supply of food is suspended for a day or two. Of course, there are a few individuals which are considerably delayed in development, and these are not able to complete moulting as soon as the others. These much-delayed silk-worms are termed "Oku-rego" (meaning "lingerers" or "laggers"), and some of them are often discarded. Therefore, appearance of many of these "lingerers" may mean in some cases, that the growth is a little slow, while it may mean, in other cases, that the vigor or health of the silk-worm is slightly affected.

It has been reported, by several investigators, that such "lingerers" were slightly more numerous in the cases where the silk-worms were reared in weak illumination than in good illumination. This point will be considered in the next section.

As to the effect of light rays of different wave-lengths on the vigor of the silk-worm, the data thus far obtained by several investigators

do not show a definite tendency. However, the difference in illumination by white light seems to have some effect.

The number of sick silk-worms which appeared when reared under various light conditions is shown in table 41. The figures in this table show the number of sick silk-worms which appeared during the total period of rearing from 1000 silk-worms with which the rearing was begun.

The results of observations by some other investigators on the number of "lingerers" and of sick larvae are shown in table 42. From the results shown in table 42, these authors conclude that the absence of sufficient illumination had an ill effect on the growth and vigor of the silk-worm. From the results in table 42, it seems rather

TABLE 42

Number of lingerers and sick larvae per 1000

LIGHT	SHADOW	VIOLET	BLUE	YELLOW	RED	AUTHOR
145	115	273	59	75	33	Tazawa (887)*
109	148	123	129	121	136	Tanabe (874)†
387	440	392	414	404	390	Tanabe (874)‡

* Tazawa, S. (887). The figures in the table show the number of the ingerers and of the sick silk-worms that appeared from 1000 initial number intil the end of the third stage.

† Tanabe, D., Watanabe, J. and others (874). Number of the sick silk-vorms and of the lingerers that appeared from 0.375 gram of the silk-worms ust hatched until the end of the fourth stage.

‡ The same authors. Experiment with another race. Number of the sick vorms and of the lingerers that appeared until the end of the fifth stage.

ıncertain whether lights of different color had a definite effect on he silk-worm.

(3) Effect on the amount of cocoon produced. As has been stated, nore sick worms and lingerers appear in the case where silk-worms re reared in weaker illumination. Therefore, the percentage of the ilk-worms which spin cocoon is smaller when reared in weak illumiation. Consequently, it may be expected that the total amount f cocoon obtainable from the same initial number of the silk-worms, s smaller when reared in weaker illumination than when reared in tronger illumination. The results of experiments by Kawara and lso the results obtained by Tanabe and others seem to support this

statement. The results obtained by these authors are shown in table 43. No definite conclusion can be drawn from the results shown in this table as to the effect of the lights of different color on the yield of cocoon.

(4) Effect on the amount of silk secreted. Observations on the amount of silk secreted by a silk-worm when reared under different conditions of light seem to be rather scarce. Some of the results obtained thus far are shown in table 44. The record in this table seems to show that a little larger amount was secreted by the silk-worm which was reared in good illumination than that reared in weak illumination. Professor Sakurai is, however, of the opinion that the difference as given in table 44 is not large enough to support a conclusion that the degree of illumination influences the amount of silk secreted. The effect of the lights of different wave-lengths can not be told from the results recorded in table 44 only.

TABLE 43

Total yield of cocoon

LIGHT	SHADOW	VIOLET	BLUE	YELLOW	RED	AUTHOR
grams	*grams*	*grams*	*grams*	*grams*	*grams*	
940.2	735.0	948	685	892	963	Kawara (464)*
622.5	570.0	637	603	620	618	Tanabe (874)†

* Per 1000 silk-worms.

† Per 962 silk-worms.

TABLE 44

Average amount of silk secreted by one silk-worm

LIGHT	SHADOW	VIOLET	BLUE	YELLOW	RED	AUTHOR
grams	*grams*	*grams*	*grams*	*grams*	*grams*	
0.187	0.176	0.176	0.176	0.161	0.150	Tanabe (874)
0.189	0.179					Sakurai (764)
0.201	0.188					Sakurai (764)

(5) Effect on the fecundity of the female moth. Observations on this point are also very scarce. The only literature accessible to the writer was the paper by Professor Sakurai. The results obtained by this author are as follows: Average number of eggs laid by the adults reared in light, 569.2, shadow, 635.0. Professor Sakurai states that

the difference in the number of eggs laid by the adults reared in different illumination is not large enough to warrant the conclusion that the conditions of illumination affect the fecundity of the adult insect.

B. Behavior and direction of growth

This subject has been very fully treated in the literature, especially by Loeb and by Mast (581). Hydroids and probably all sessile aquatic animals grow toward or away from a source of light just as plants do. Many animals orient to direction of rays. Many animals select light of certain intensities, and exposure to light may change the reaction to light.

Light, in combination with certain temperatures, is essential to egg laying of codling moths. Isely and Ackerman (428) and Garrett (323) believe that this may control abundance of the moth and hence degree of infestation of apples.

Lower vertebrates and invertebrates are able to distinguish colors (718) and even ultraviolet (541).

IV. POLARIZED LIGHT

The results obtained by Semmens (792, 793) indicate that in investigating the effect of light polarized light should be considered. Moonlight is regarded as being partially polarized light. In samples of seeds exposed to moonlight, and sunlight, those exposed to the moonlight germinated better than the others. Starch grains were dissolved under polarized light, but only very slowly so under ordinary sunlight, and not at all in the dark. The effect of the polarized light from the sky is not emphasized.

Semmens showed that polarized light thrown upon a living leaf will stimulate the dissolution of starch grains, and found further that polarized light is responsible for the opening and closing of the stomata as the daylight changes; that is, for some hours after sunrise the light received by the earth from the sun is partially polarized and grows less so towards midday, and again as the sun sinks towards the horizon the light once more becomes of polarized character. Crozier (227) failed to find any effect of polarized light upon certain animals.

V. EXTRACLIMATIC RAYS

Physiologists have used commercial lights, such as the mercury arc, without regard to the limits of the sun's spectrum and often without inquiry as to the specific wave-lengths which gave the effects obtained. Extraclimatic rays were involved in this work.

The far ultraviolet (290 $m\mu$ to 100 $m\mu$) usually has pronounced effects on organisms. Division in Paramoecium is retarded by long exposures to wave-lengths under 280 $m\mu$ but the after effect of short exposures is an increased rate (165). Only a few determinations of specific wave-length effect in the far ultraviolet have been made. Recently exposure to short wave-lengths has been used to modify the heredity mechanism.

X-rays, in quantity, have a harmful effect upon healthful tissue, producing painful sores that refuse to heal for months. X-rays kill first the active dividing cells, and it is because of this selective effect that X-rays can be used in destroying certain cells during development, reproduction and growth, and in treating certain diseases. X-rays have been used on cancer; they sometimes check the disease, but they cannot cure it. In rodent ulcer, a somewhat similar disease in rats, X-rays may effect a cure. X-rays have been used successfully in treatment of skin diseases, such as ring-worm. In X-rays treatment it is necessary to measure the dosage carefully, as too much is harmful.

While X-rays are an extraclimatic factor, it is noteworthy that large doses kill the meal-beetle (*Tribolium confusum*) at once; smaller doses cause the animal to die some days after treatment; still smaller doses have been shown to increase the life of the beetle (238). Recently investigators have changed the color of mice (Hance (512)) produced various defects in mice (Brogg and Halter (512)) and controlled rate of mutation (Muller (512)).

CHAPTER XIV

Measurement and Control of Light

I. INTRODUCTION

The kind of light measurement to be made in climatic simulation work should be determined by the responses of organisms. Light is at present one of the most difficult factors to measure or control. White light or day light is composed of many wave-lengths characterized by visual sensations of color, and of near ultraviolet and infrared which are invisible. These wave-lengths have direct and specific effects upon organisms, especially animals, and indirect effects upon the quality of their food. Those methods which make possible the measurement of the energy of the entire spectrum and intensity (energy) of the different wave-lengths or groups of wave-lengths are logically advocated from the view point presented. This involves electrometric measurement and quartz prisms, gratings, screens, total-energy-receiving instruments and photo-electric cells. An added important reason for restricting one's efforts to these fields of measurement, lies in the fact that all may be utilized in the control of light in experiments and in continuous recording of light conditions in experiments and in nature.

The use of photographic and visual methods can hardly be advocated, for even the spectrophotometer cannot be used without time-consuming photography, inasmuch as the near ultraviolet, which has important specific effects on animals, is not visible.

Qualitative measurement can hardly be omitted at any time, because the intensity of the white light may vary while all wave-lengths remain of approximately the same *relative* intensity, or the relative intensity of the different wave-lengths may vary while the intensity of the wave-lengths used in measurement remains about the same. There is nothing accurate about intensity or quantity as ordinarily measured by selective methods covering a wide range of wave-lengths. Rays having important effects are commonly omitted from consideration, or heat, visible light, and ultraviolet light are measured together. Roughly speaking, however, intensity or quantity is meas-

ured with reference to normal sunlight and usually based on the sensitivity of the eye.

The quality of light is also mentioned when differences in wave-lengths present are considered. Where the different wave-lengths are measured separately by means of screens, prisms, or gratings, the measurements are sometimes said to be quantitative with respect to wave length.

1. *Measurement*

All measurements of light should be reduced to calories per square centimeter per minute. This is the standard term for expressing the energy of the sun's radiations and in biological work where surfaces of animals are exposed. All selective and relative methods should be standardized or standardizable in these terms.

Bolometers or thermopiles measure light as energy and are commonly standardized in this way, which is accordingly the basic method of measurement. They may be used to measure a very restricted portion of the sun's spectrum as well as the total effect of heat and light. All selective radiometers should be standardized on this basis. This is not, however, always easy. Selective radiometers with sensitivities such as shown in figure 136 (Chapter XIII) may show the same energy reading with considerable variation in the position of maximum intensity of the light measured. They must accordingly be used with discretion, i.e., standardized with reference to each type of light used. There will in many cases be difficulty in restricting the sensitivity of the thermopile to the same wave-lengths and relative sensitivities as the selective radiometer. Such methods are, however, infinitely better than those commonly used.

In the measurement of light intensity there are four principal methods. The first (energy method) has just been mentioned. The second is dependent upon the eye, directly or indirectly, and involves what is known as intensity and color. The third is dependent upon photochemical reactions, chiefly in photographic plates and papers. The fourth method of importance is the use of photo-electric cells, which are in no case sufficiently sensitive in the red to be of value for its measurement. They have to be carefully screened to secure approximately equal responses from all other wave-lengths. They have the advantage, however, of being insensitive to heat.

The quality of light, or the intensity of its different wave-lengths, is measurable with the same equipment as its total intensity, or quantity, but with the addition of screens, gratings, or prisms which separate the wave-lengths.

Since there are many circumstances in which investigators must use equipment already available, or have inadequate resources, time, and training for the development of electrometric methods, other methods are elaborated here, whereas they otherwise would be ignored in favor of methods that can be used in light control in experiments as well as in measurements.

II. MEASUREMENT OF INTENSITY

1. *Thermopiles, bolometers, etc.*

The thermopile consists of one or more "junctions" of different metals, iron and constantan (or better, two alloys of bismuth-antimony and antimony-cadmium) arranged so that one set of similar junctions can be exposed to radiation while the other set is protected. They may be made to show as much as 25 millivolts in full sunlight. To increase the amount of radiant energy intercepted, the exposed junctions are covered with blackened, silver or copper disks, and similar disks should be put on the unexposed junctions. If the final elements are connected by wires to a very delicate galvanometer, very slight changes in temperature of one set of junctions, of the order of $\frac{1}{1,000,000}$°C. or less, will produce a readable deflection, and will correspond to a very weak stream of radiant energy falling on the exposed junctions, such as, for example, the radiation from a single candle at a distance of 50 meters. To be quick acting and sensitive the mass of the junctions should be small.

A bismuth-iron thermopile made by J. P. Foerst in Dr. C. E. Mendenhall's laboratory at the University of Wisconsin is very sensitive and gives nearly 30 millivolts in full sunlight. It, however, shows a considerable lag when exposed to increasing or decreasing light. A copper-constantan thermopile from the same source (pyrlimnometer of Birge and Juday (88)) gives about half the deflection, and is less delicate. Either of these can readily be calibrated at any of the United States Weather stations having a total energy recorder.

These instruments are prepared for use under water and contain a moisture-absorbing salt which is effective for several years. Readings can be taken under water without special precautions (see page 457). For any purpose, however, the transparent window should be of quartz. For out-of-door readings, where comparative results are the chief desire, readings of visible light (heat screened out) may be made in air by suspending the thermopile in a white vessel of distilled water so that it is covered with a layer of water 1 cm. thick, with a heat absorbing glass (Corning G392 H) in place. In addition, other screens may then be used to measure the energy of portions of the spectrum. These instruments may be read on Rawson unipivot galvanometers and on millivoltmeters.

Burns (136, 137) has used a vacuum thermocouple and read the permanent temperature produced by the radiation, on a potentiometer.

In the Kimball pyrheliometer (Kimball and Hobbs (473)) used by the United States Weather Bureau, the junctions are arranged in two circles, one under a white and one under a black ring of thin copper.

Klugh (481) mentions a pyrheliometer made by Jules Richard of Paris, which is semiportable and calibrated in calories per cm^2 min. Klugh found it sufficiently sensitive for biological work.

The bolometer is a very sensitive instrument. It consists of two similar strips of very thin (0.001 mm.) platinum mounted side by side, having exactly the same resistance, and arranged in a Wheatstone bridge, so that any unequal changes in resistance of the strips can be measured. One strip is blackened and exposed to radiation which causes its resistance to change.

2. Photo-electric cells (186, 275, 495, 502, 505, 681, 791, 836)

All metals emit electrons under the influence of light. This emission depends upon the kind of metal, upon the condition of the surface, and upon the surrounding conditions. In most cases the emission is almost imperceptible. By using a very active metal, such as strontium, rhubidium, caesium, lithium, sodium, or potassium, and placing it in a vacuum or, much better, in an atmosphere of helium, hydrogen, or argon, the photo-electric effects become very considerable with a potential of 20 to 300 volts across the cell.

Photo-electric cells are of two types, (a) vacuum and (b) gas-filled. Both are essentially independent of temperature and other surrounding conditions.

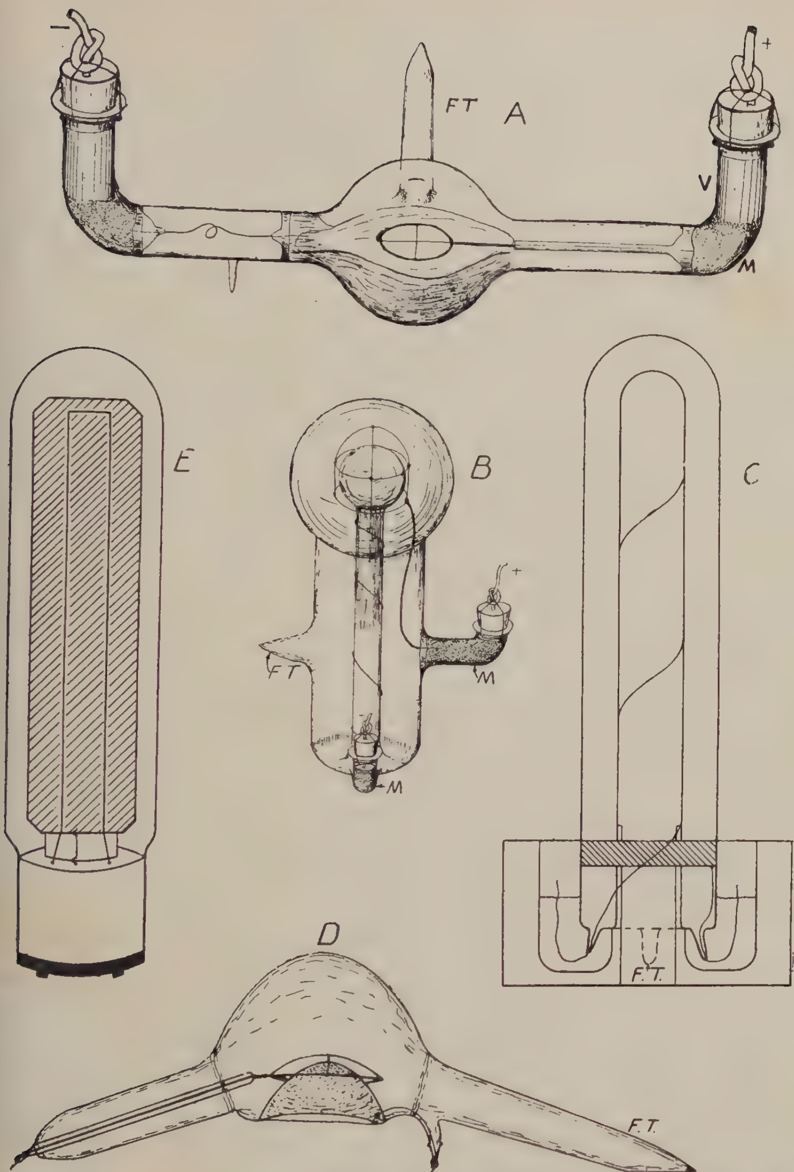


FIG. 137. Forms of photo-electric cells (504): *A*, wide apertured subaquatic cell. *B*, double sphere cell; only the inner sphere should be sensitized but usually the stem was unavoidably covered also. *C*, double cylinder; only the inner cylinder was coated; the positive electrode consisted of a very thin silver mirror. *D* is a convex cell; only the center hemisphere was covered with sensitive metal. *E*, case cell with metal deposited on a nickel plate. The letters on the cells have the following meaning: *M*, mercury; *FT*, filling tube; *V*, vaseline.

a. Vacuum cells. The vacuum cells give a current proportional to illumination only over a short range of light intensity. The Case cell is an exception, giving proportional results over all ranges up to full sunlight. In this cell strontium is deposited on a flat plate. Vacuum cells are only slightly influenced by changes in voltage above 150 to 300 volts, depending on the cell. These cells are reputed to be more stable than the gas cells, i.e., to give the same current in the same light intensity more often.

b. Gas-filled cells. Gas cells are sensitive to all wave-lengths except red, but only slightly sensitive to yellow and extreme ultra-

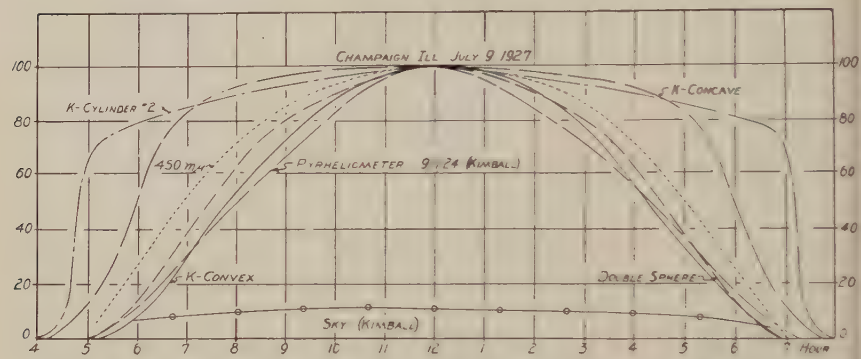


FIG. 138. Curves of relative response of potassium cells of different forms 40° north latitude July 9, 1927, from a Leeds' and Northrup recorder carrying six cells. The cylinder partakes of the effect of a vertical surface. The double sphere and convex all are nearest the ideal calculated sun values shown by the curve marked 450 mμ. The convex cell is better than a flat surface. The curve of the concave cell shows the effect of the extreme sensitivity to blue which characterized this particular cell.

violet. The maximum differs with the alkali metal, beginning at about 340 mμ, the order being sodium, lithium, potassium, rhubidium, caesium, and ending at 540 mμ (see fig. 144). Some sodium cells and some potassium cells show a secondary maximum in the ultra-violet. In two potassium cells showing this, one in quartz was below 290 mμ and one in glass was at about 370. These peculiarities do not characterize cells made from pure metals. Other cells from the same and other metals showed a gradual decrease from their blue-green maximum to 300 mμ where the glass cut off shorter wave-lengths. Some carefully made sodium cells have the maximum at about 420 mμ (791).

The form of the cells is of much importance. A number of forms have been tried (831). The first of these were made for use behind the astronomical telescope and had the general form of the eye. Obviously, this is not a correct form for biological work. Much of

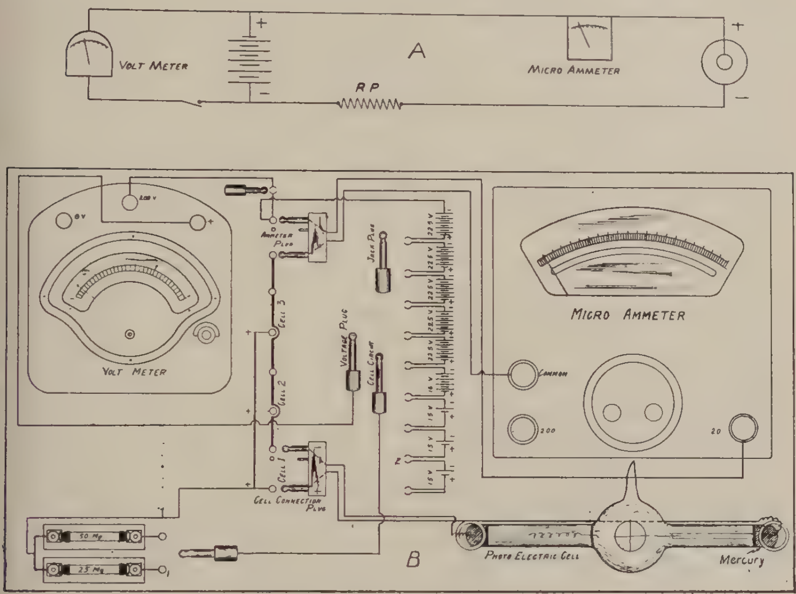


FIG. 139. *A*, a simple wiring diagram for one photoelectric cell shown at the right. *R-P* is the protecting resistance. *B*, wiring diagram for the field box shown in figure 140.

The batteries (*B*) were connected by inserting solid plugs into the telephone (*J*). The batteries have a series of cells which may be added in $1\frac{1}{2}$ volt steps thus insuring the desired voltage within less than $1\frac{1}{2}$ volts. The voltage could be read by inserting the volt plug (*V*) in connection with the last cell and inserting another solid plug not shown, to connect the negative pole with the voltmeter (see fig. 140, *B*). The high resistance meter rendered the voltage readings stable. The micrometer is shown at the right. The cover (*C*) could not be raised until all plugs were withdrawn after which the space between the microammeter and the bakelite panel (*P*) could be used for storage. Large sized *B* battery aggregation upwards of 100 volts may be readily carried. A smaller case may be readily fitted up.

the difficulty was overcome by making the spherical portion large and coating only the lower third, as shown in Figure 137, A. Mercury cups were added to insulate contacts. A spherical sensitive part would seem ideal. Eight of these were tried, but with one exception they either broke while at rest, leaked, or were too insensi-

tive. Double cylinders were also tried with much better success, but they appeared to partake too much of the properties of a vertical surface, which may have reduced the noon maximum. One convex type cell was made but was not as sensitive as the others, and com-

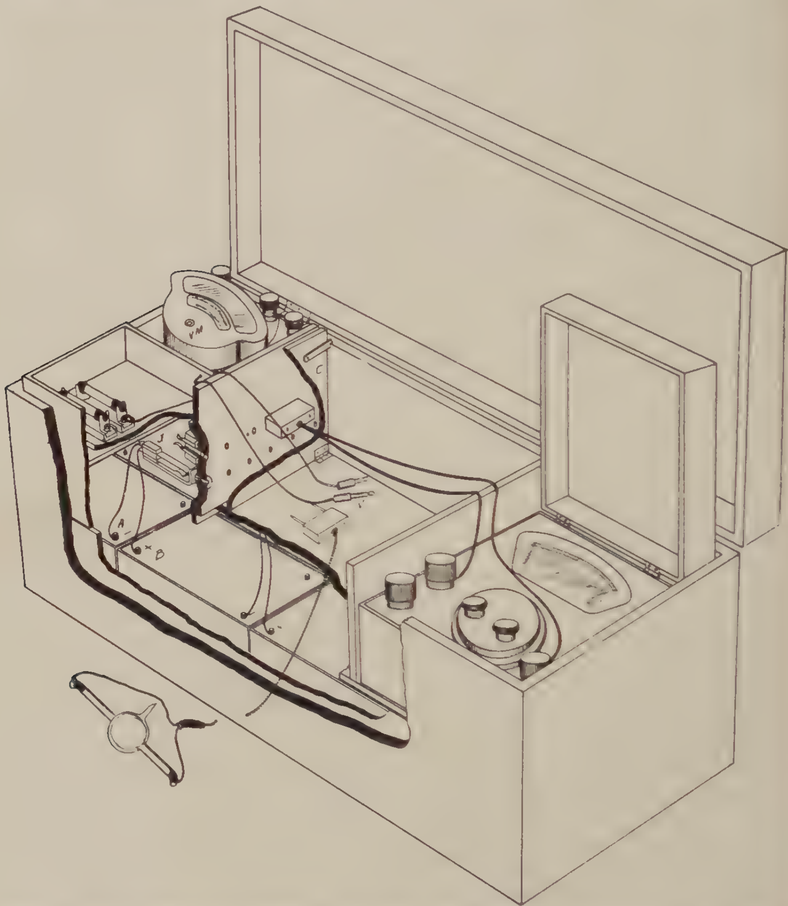


FIG. 140. Battery and switch box used with the photo-electric cells (831)

parisons were rendered difficult. Figure 137, *A*, *B*, *C*, *D*, *E*, show the various forms of cells in use for sunlight measurement. Figure 138 shows the curves for cells of different form.

The cells have been standardized to sunlight intensity by reading

the light intensity with the Macbeth illuminometer. The illuminometer readings were taken while the sunlight was reduced to definite percentages by a sector disk on clear days, principally in June. A sector disk 45 cm. in diameter was rotated over a light-tight box which could be tilted so as to face the sun at all times.

The electrical connections for use with the photo-electric cell are shown in figure 139, *A*. For field work they must be kept simple so the equipment may be light and the current still readable on a portable microammeter. Engineers are likely to advocate amplification, but this is undesirable as it adds weight. The difficulties of too small current may all be overcome by making larger and better cells, thus leaving the weight to be carried at a minimum.

Batteries, a high resistance voltmeter, and some form of galvanometer are necessary; the circuit is simple, as shown in figure 139, *A*. In the writer's work the batteries were carried in a box or case which protected them from moisture (fig. 140 and fig. 139, *B*), (831). Burgess B batteries were connected to telephone jacks mounted in a bakelite panel in such a way that solid plugs could be used to connect battery cells or groups of cells together and give any desired voltage (figs. 139 *B* and 140). The voltage could be read quickly by means of a small Weston battery voltmeter of high resistance. The panel was so wired that a photo-electric cell could be connected in the circuit by inserting a two pole plug attached to the cell's cable. The reading instrument was connected into the circuit in the same manner. The two arms of these plugs connected with telephone jacks. All conductors were carefully insulated except on the contact surface. One purpose of using the jacks and plugs was to make possible the covering of the self-cleaning contact surfaces with vaseline and the complete separation and drying of all parts if leaks should occur in a moist atmosphere. Two Daven tubular resistance units, one of 250,000 ohms and the other of 500,000 ohms, were available in the set; changes could be made by shifting a plug.

The instrument used for the reading was a Rawson single pivot ("acrid") micro-ammeter with two ranges of 200 and 20 microamperes, respectively.

3. Provisional Methods

a. Instruments using the eye (482, 702). The maximum sensitivity of the human eye is at about 551 mμ (in the green). It differs

FIG. 141. The Macbeth illuminometer in use (see fig. 148, p. 352). (Courtesy of Leeds and Northrup Company.)

with the intensity of the light, and with the individual, and is about half way between the extremes for the maximum energy of the sun at different zenith distances. These facts are important in judging the intensity of light of different colors.

There are two important photometers dependent upon the eye,—the Sharp-Millar (801) and the Macbeth illuminometer (fig. 141). Light is measured by comparison of a white surface illuminated by the sun or other source by means of a Lummer-Brodhun cube (Swan's double prism, 1859). This piece is a cube made up of two prisms. An area in the center of the meeting faces is clear for the passage of a beam of light while the periphery of the area is opaque but mirrored from one direction. Two beams of light are admitted at right angles to each other; one is transmitted through the center of the cube, the other is reflected parallel to it and surrounding it. The observer sees the transmitted light in the center and the reflected light surrounding it. The latter is moved to or from the cube until the two are indistinguishable when the color of the two lights is the same. When not the same, most satisfactory results may be obtained by using the position when the boundary between the two fields is most indistinct. The Macbeth illuminometer is an improvement of the Sharp-Millar and made completely portable (see fig. 141), The Leeds & Northrup Macbeth illuminometer consists of five essential parts; the illuminometer including the working standard lamp, controller, reference standard, and test plate—all contained in a carrying case and weighing about 17 pounds.

The illuminometer is shown in hand in figure 141. A Lummer-Brodhun cube is mounted in the rectangular head. The aperture opposite the telescope is pointed toward the test plate. In the tube is a diaphragmed carriage, within which is mounted an electric incandescent lamp (working standard). The lamp carriage is moved up and down in the tube. On one side of the rod to which the lamp carriage is attached, there is a direct reading scale in foot candles: 1–25.

The controller comprises the two dry batteries for operating the lamps, a Weston milliammeter, two close regulating rheostats, one for the working standard and one for the reference standard lamp, and a double throw switch by means of which the milliammeter may be brought into either the working standard circuit or the reference standard circuit. The reference standard may be used to check

the working standard at any time or place. Frequent calibration permits the use of working standard lamps at high efficiency and eliminates personal errors.

The test plate is of glass (white) finished by a special process, showing practically no error up to an observation angle of 25 degrees, and from that point the error is much less than the other materials. These plates may be washed with soap and water.

Absorbing screens made of so called neutral glass, which may be placed on either side of the Lummer-Brodhun cube, extend the range of the instrument (ordinarily 0.02 to 1200 foot-candles). The range may be increased by additional screens, two or three thousand times maximum and minimum if desired. For measuring sunlight, a blue-violet absorbing screen is provided which reduces these colors on the test plate to match the standard lamp. The readings have to be approximately doubled when this screen is used.

In making measurements in forests and of reflection from water surfaces a horn may be used. This horn consists of a metal elbow, screening diaphragms and a mirror set at 45 degrees. This attachment may be slipped over the illuminometer viewing tube. To take into consideration the absorption of light by the mirror, a separate comparison with the reference standard must be made and a new current value used with the working standard lamp.

Some users reserve the reference standard for work at a distance from laboratories and standardize their lamps in a photometry room. To do this, the test plate must be fastened to the carriage so as to be squarely in front of the standard lamp. Its distance is then adjusted on the photometer bar so as to give 3 foot-candles illumination. The current of the illuminometer is then adjusted to make the intensity from the working standard match.

A probable improvement for sunlight measurement might be brought about by using a larger lamp and screening it with daylight glass to match the plate in average noon sunlight. The large energy loss with screens to produce noon sunlight would necessitate increasing the voltage and capacity of the controller as well as the size of the illuminometer parts.

b. Selenium cell (117, 118, 250). Selenium cells are commonly made by connecting several narrow strips of light-sensitive selenium parallel between the edges of two brass plates. The resistance of such a cell depends upon the construction and the treatment (often

by heat) of the selenium. It is very difficult to make duplicate cells and they must be operated at constant temperature.

c. Photochemical methods. This type of light measurement is carried on mainly with photographic papers and plates, though other chemical reactions have been used. In photographic methods, either plates or films which require development or papers which show the changes at once may be used.

(1) Papers. The use of the papers really consists in (a) measuring the *time* to match a standard tint or density as an index of light intensity and (b) using neutral wedges, the intensity of light being measured by the distance to which the color extends from the thin toward the thick end of the wedge with a fixed exposure, as compared with some standard light. A suitable high intensity source may be fixed as one which will make the change barely visible at the thick end of the wedge. The light in some location to be measured is estimated on the basis of the distance at which the change is just visible. The wedge principle was utilized in some of the earliest photometers. The neutral wedge was long since used in stellar photometry. According to Klugh (481) neutral wedges suitable for habitat work are of two kinds; made from dark colored glass or made by placing wedge shaped pieces of gelatine stained with a neutral dye such as nigrosine between two strips of optical glass. The gelatine wedges are made by the Eastman Kodak Company in various gradients. Klugh recommends rhodamine B paper for use with the wedge. It is sensitive to red.

The work of Bunson and Roscoe in 1862 is quoted as an important beginning in the method of photochemical photometry. A large number of photometers have been devised for use with photographic papers. Several are recording, and at least one uses the wedge principle. These instruments have appealed to field botanists and ecologists, and there are numerous reviews of such instruments. Weisner (96) developed an instrument and a technique. His arbitrary standard was the light required to change the paper to a standard tint in one second.

Clements (173) describes one designed and used by himself. He finds a stopwatch of high excellence necessary. With all such photometers, it is best to have the mechanism which exposes and covers the paper start and stop the watch. This is evidenced by Weisner's one-second standard. Various photographic exposure meters have

been used for the measurement of relative intensity. Usually papers are most sensitive to the blue-violet and solar ultra violet (707).

Pulling (707) discusses measurement in general. Przibram (706, in Abderhalden's Handbook) describes Vouk's paper photometer in which the paper is operated like the film in a kodak, and the Eder-

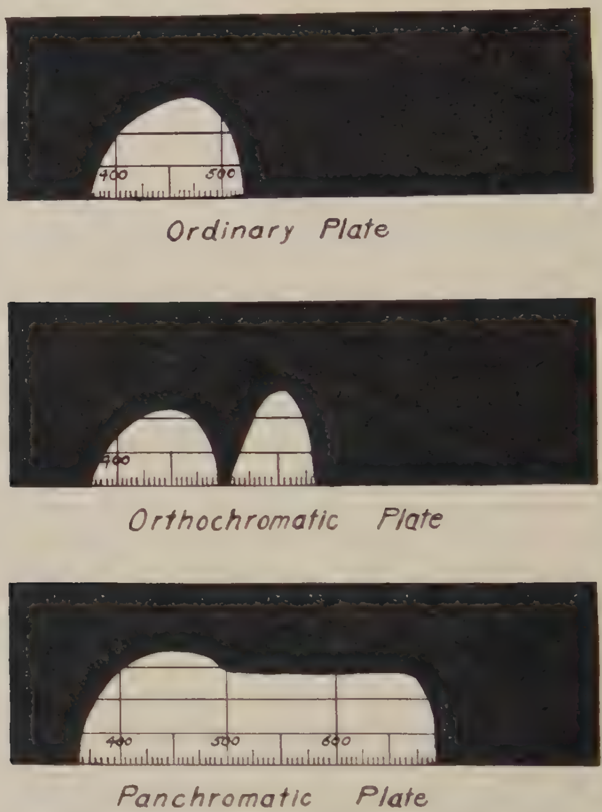


Fig. 142. Wedge spectrographs of three kinds of plates (United States Bureau of Standards).

Hecht's neutral wedge photometer, and also cites the original descriptions. Braid (111) discusses actinometers and various photochemical methods critically. Color screens are often used with papers, and papers are or may be made nearly isochromatic.

(2) Plates and films. Plates have long been used, especially for

he ultraviolet, as in stellar photometry, spectrophotometry, etc. Panchromatic plates are made nearly equally sensitive to all wave engths (Davis and Walters, 240). Other types are distinctly elective (fig. 142). Klugh has recently discussed this subject in letail (480). Errors arise from the thickness of the glass (480). Plates are usually not quite isochromatic (240), and after all is done nd the plates are developed, the density of the plates must be deermined. For this purpose numerous methods have been employed: omparison with standard densities prepared in advance, rotating ector disks, wedges, filters etc. Various instruments employing hese or other principles are called densometers (187, 456, 457, 458, 67, 784). Finally, microphotographs have been made and the silver particles counted for unit areas where the negative is very thin. The density varies directly with the logarithm of the exposure for noderate exposures, and differences in density as expressed differ umerically essentially as the logarithms.

III. RECORDING SUNSHINE AND LIGHT INTENSITY (672)

1. Pyrheliometers, bolometers, etc.

These are used for recording light by merely attaching to a recording millivoltmeter, recording potentiometer, or recording Wheatstone bridge. They are the standard instruments for recording light. The Kimball pyrheliometer has been used and compared with the Sharp-Millar photometer with a good agreement between the two (Kimball, 471).

2. Photo-electric cells

Continuous recording of light intensity has been accomplished by neans of photo-electric cells and recording potentiometers. If a pecial resistance coil is supplied for each cell, the drop in potential cross this coil when in series with the cell is directly proportional o the current.

The form of the cells used is especially important here. Figure 43 shows the wiring diagram of six photo-electric cells used in ecording light. It is merely a group of parallel connections across generator and protecting resistance with all cells except one openircuited at any moment. The drop in potential across a special

coil is measured and recorded in millivolts by the recorder. Within limits the cells may be made to read alike by reducing the resistance of the special coil for the cells giving a large current and increasing it for those giving a small current, and varying voltage and protecting resistance.

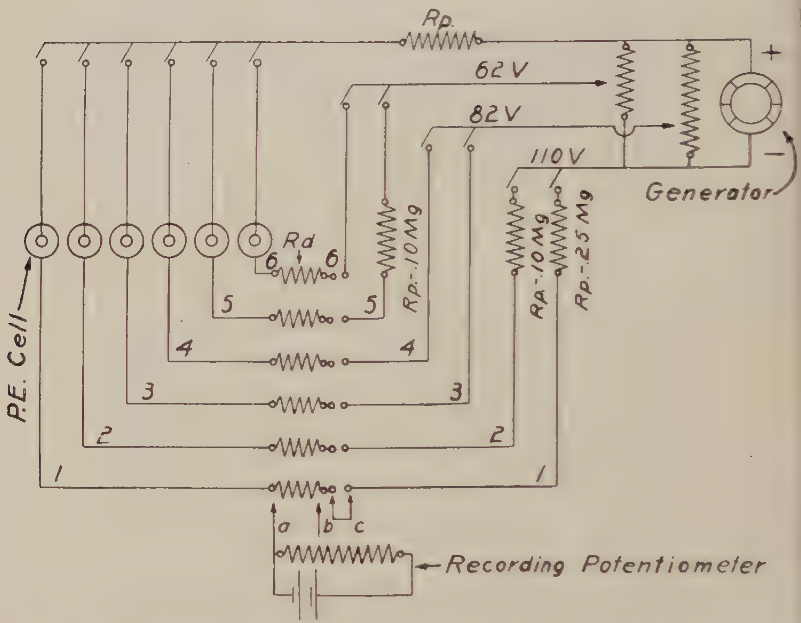


FIG. 143. Wiring diagram for six photoelectric cells with different drop resistances (*R d*), different protecting resistances (*R p.*) and three different voltages.

3. *Provisional methods*

Photographic papers, black-bulb thermometers and black evaporimeters have been used for the recording of light intensity.

a. Sunshine recorder. Sunshine recorders are of several types. The Campbell-Stokes sunshine recorder consists of a 4-inch crown-glass sphere which focuses the sun on a card and burns a line on a printed scale. The Jordan sunshine recorder admits sunlight through a small aperture where its effect is recorded on a sensitized paper. In the United States Weather Bureau type, a black-bulb thermometer is enclosed in a vacuum tube to eliminate the effects of atmospheric

emperature. Two separate platinum wires are fused into the center of the mercury column. The expanded mercury completes an electric circuit and activates a mechanism which brings the recording pen into contact with the revolving drum.

b. Atmometers (523, 527). Black and white atmometers have been used to measure radiation. The difference is expressed in cubic-centimeters of water evaporated. The work of Adams (1921), on Mount Marcy, showed that the black bulbs evaporated roughly twice as much as the white ones. It should be possible to calibrate these with a thermopile, but as this has not ordinarily been done the results are usually relative (see p. 303).

c. Photographic paper intensity recorders. The Samec and Jencic recorder (Przibram (706)) rotates a drum covered with sensitive paper exposed through small openings arranged from top to bottom of the drum. One opening gives full exposure and the others grade off in a series to almost complete opacity, thus giving a sharp wedge effect. This gives a triangular area for each sunny day. Lundegardh (Klugh (480)) developed a machine using a neutral wedge in the same general manner. Clements' selagraph operates a wheel carrying sensitive paper past an exposure slit opened every half-hour. The wheel carries azio paper for cloud and shade and solio for sun and bright illumination. The instrument runs for a week without attention.

IV. MEASUREMENT OF QUALITY OF LIGHT (330)

The measurement of the quality of light is conducted essentially as is the measurement of intensity except that different wave-lengths or groups of wave-lengths are measured separately by interposing prisms, gratings, or screens, to separate or shut out certain rays.

1. Thermopiles, bolometers, etc.

The thermopile or some similar instrument may be used to determine the energy of each particular wave-length or group of wave-lengths projected onto it from a prism or through a screen. To measure the energy of the visible light requires a screen which cuts out all heat without acting selectively on the light. For this purpose 1 cm. of water and a piece of heat-absorbing glass (Corning G 392 I) have been used.

2. *Photo-electric cells*

The photo-electric cell is one of the most promising instruments for the measurement of ultraviolet and visible light except the red and orange. The red and infrared are eliminated through insensitivity. Unfortunately, the ultraviolet sensitivity of these cells has been studied but little. The sensitivity of sodium, lithium, potassium, caesium, rubidium, and strontium cells is well known from about 340 mμ to their limit in the yellow or orange. Cells from different alkali metals differ in sensitivity (fig. 144). The maximum range is from 340 mμ for sodium to 540 mμ for caesium. The chief work

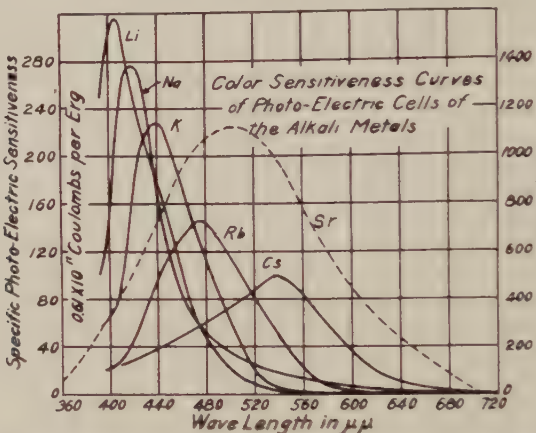


FIG. 144. Color sensitivity of photoelectric cells from various metals. The (Case) strontium curve is not to scale. The maximum for *pure* sodium is 340 mμ. The figure is from Seiler (791; see 832) with strontium added.

in measuring light with these instruments and segregating different colors has been done for biological purposes, also possibly in astronomical studies (Shelford and Kunz, 831, 832).

The most promising use for the cell is in the study of the short wave-lengths with green, blue, violet, and ultraviolet glass and screens such as silver on quartz plate (figs. 145–147). Figure 136 shows sensitivities after screening. Such glasses as noviols and reds may be selected to cut off the shorter wave-lengths at any desired point until red alone is left. These instruments are barely sensitive to wave-lengths greater than about 610 mμ.

Richardson and Young (732) have recently made sodium cells temporarily sensitive to the long wave-lengths including infrared, by

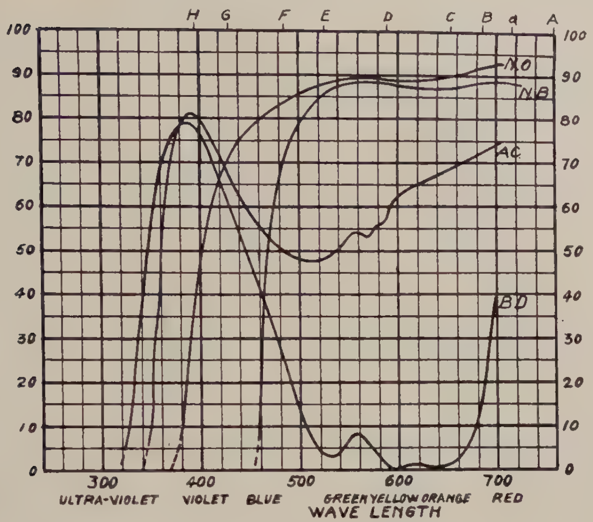


FIG. 145

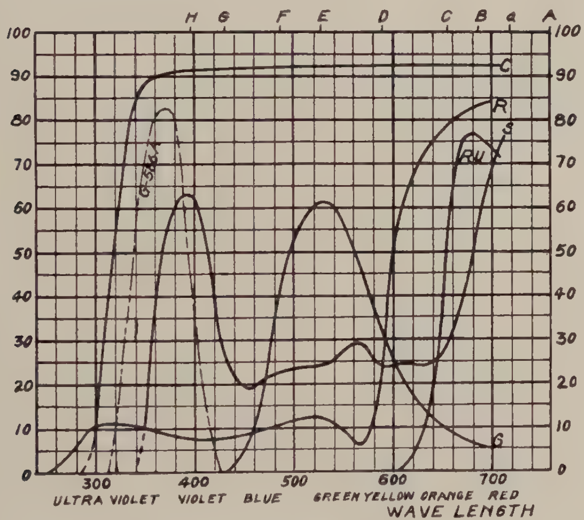


FIG. 146

FIGS. 145, 146. Per cent of light transmitted through various glasses (United States Bureau of Standards (332, 331)). *N O* Corning Noviol O; *A C* Amethyst C (Am. Op. Co.); *N B*, Corning Novoil B; *B D*, Blue D (Am. Op. Co.); *C*, Crown glass (Am. Op. Co.); *R*, Copper Ruby (Jena); *RU*, ruby; S, Smoke (Am. Op. Co.); *G*586 a (Corning); *G*, green.

sensitizing with water vapor and sulphuric acid. When screened with a selected red glass, a caesium cell has a low sensitivity to orange from 570 to about 640 depending on the cell. Using a yellow glass, the maximum is at 550 and the strongest effect is in the orange (fig. 136, p. 318). Well-selected green glass restricts the rhubidium cell to green light, while noviol (fig. 145) cuts out the shorter wave-length blue. Blue glass restricts the important part of the sensitivity of K cells to blue (fig. 145, *BD*). (*Cf.* fig. 136, p. 318 and fig. 192, p. 546.)

For the ultraviolet, potassium, sodium or lithium cells and Corning G986A and 586A confine the sensitivity to near ultraviolet and visible violet in varying degrees (figs. 144 and 147) providing the

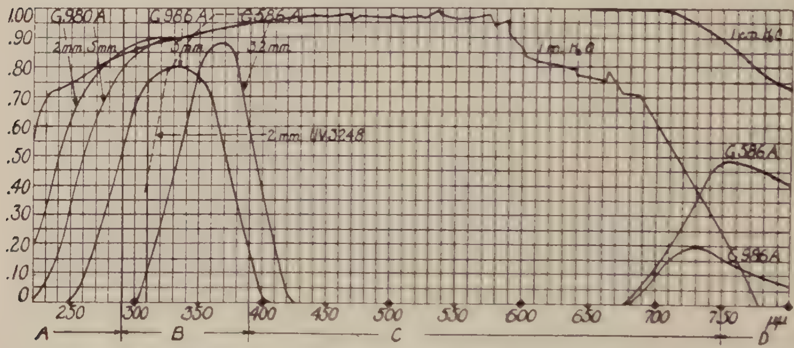


FIG. 147. Transmission of water and various glasses (Glass from (319). C. 980 A is a Corning glass transmitting beyond the sun's limits and, in 2 mm. thickness, it transmits 85 per cent. of 290 mμ. G 586 A and G 986 A are Corning glasses; U. V. is Jena Uvoil.

cell is made of a correctly transparent glass or quartz (319, 331). Advantage may also be taken of the peculiar transmission of the copper red glasses and the didymium glasses. The sensitivities of photo-electric cells in the ultraviolet have not been sufficiently studied; two of our K cells showed double maxima in the ultraviolet. One quartz K cell showed a sharp rise at the limit of the sun's ultraviolet. These abnormal properties may often prove useful.

3. *The continuous recording of light quality* (S32)

This may be accomplished with several properly screened photo-electric cells recording on a Leeds & Northrup multiple-point potentiometer recorder. Figure 143 shows the wiring. A type of cell

designed for giving the best record of light as received by plants and animals may be screened to measure various portions of the spectrum as suggested on p. 318. Figure 149 shows the result of a half day's record with screened photo-electric cells. These were all the sub-aquatic type of cells placed in brass cylinders and covered with glass. The sun reached the sensitive surface with a zenith distance of about 40 degrees (8:30 and 3:30) and gave a maximum illumination of the same at 25 degrees (10:40 and 1:20). The difficulty with the form is illustrated by the yellow curve which eliminates the excess of sky blue. A sharp rise began at 8:30 and continued to 10:40. The striking sky effects are shown in the blue and violet. Sky effects are also noteworthy. These curves are based on adjustment of voltage and resistances so as to give about the same reading for all cells near the time of maximum. For practical recording such cells should be carefully standardized against a bolometer or thermopile screened so as to eliminate heat and have about the same sensitivity curve as the cell being standardized. The drop resistances may easily be adjusted so as to give correctly proportional readings at noon on clear days.

4. Provisional methods (480, 481)

a. The eye. The eye is sensitive to wave lengths which are recognized as color. Short wave-lengths to 386 are recognized at ages eleven to twenty, to 402 at ages sixty-two to seventy. The difference is due to the increased absorption by the eye.

(1) Spectrophotometers. There are various spectrophotometers dependent on the eye. Clements uses a portable spectrophotometer to analyze the light and forest shade. (For a discussion of these, see Knott, 482). Some of them use the Lummer-Brodhun cube (fig. 148) and are entirely similar in principle to the Macbeth illuminometer (which might be elaborated to cover this field.) However, the light coming to the eye-piece is passed through a prism so that the colors of the two sources may be compared, one at a time, by shifting the eye-piece with reference to the prism (fig. 148). Screens may be compared against two like lights, or any light source may be compared with the standard lamp calibrated as to intensity by wave-lengths by means of a thermopile. Equalizing the two lights may be accomplished by a pair of nicol prisms, a variable slit or a rotating sector disk. All these instruments, being limited to visible rays,

cannot take account of the near ultraviolet which has important effects upon organisms.

For student work, perhaps the simplest instrument for qualitative examination of lights and screens, was designed by Dr. J. Phelps Gage of the Corning Glass Works. It consists of a Spencer pocket spectroscope with a comparison prism set in front of it and the assembly mounted obliquely on a stand with two (for examination of screens) similar frosted-glass light bulbs placed about equidistant on

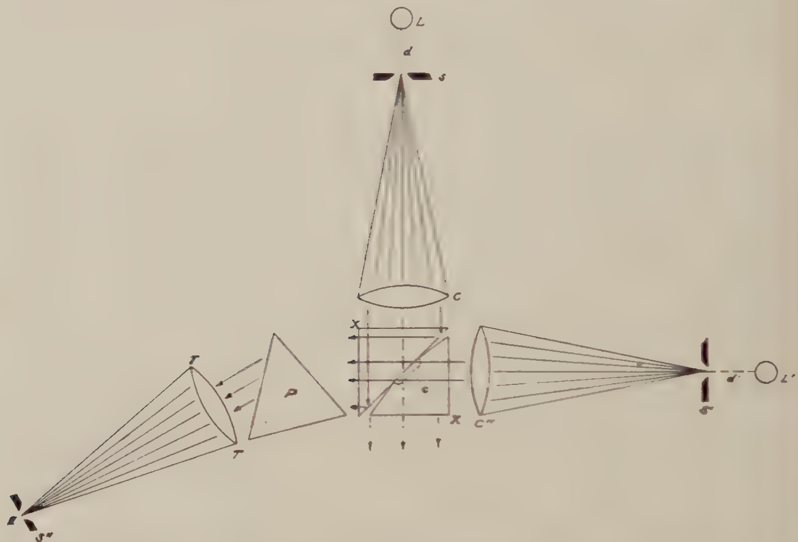


FIG. 148. The Lummer-Brodhun cube as used in specrophotometers. L and L' are two lights to be compared. L' appears in the centers while L is seen (after reflection) surrounding the light from L'. This cube without the prism is an important part of the Macbeth illuminometer.

the right and left. The two spectra are seen side by side. The writer has developed one of these in which the left-hand light is fixed at 10 cm. distance with a few centimeters latitude for parallel adjustment. The right-hand light is free to be moved along a board 2 meters long marked in centimeters. With the movable lamp so adjusted that the two spectra appear identical, the student places a screen over the fixed lamp, notes the colors absorbed or reduced by the screen, then estimates the effect of the screen on the reduced primary colors by moving the right-hand lamp away until the intens-

ity of the color being examined appears the same in the absorption and unmodified spectrum. The reduction of the intensity of the color is then estimated by recourse to the law of squares. The same equipment may be used for comparison of light sources used in experiments for class work. The quantitative estimations are very rough and the quality often bad, due to reflections.

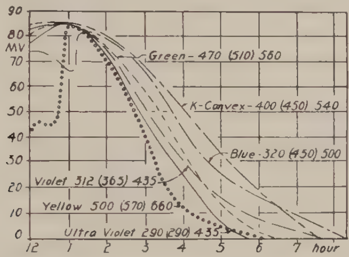


FIG. 149. Showing the continuous record of six screened cells on a Leeds and Northrup recorder (see figs. 136, 192 for transmission curves). Read in order from bottom at 5:00 p.m. the cells are: *Cs* screened with high transmission yellow (Corning); *K*, (quartz) screened with G 986 A (Corning); *Rb*, green glass; *Na*, G 586 A (Corning); *K*, blue; and K convex unscreened. Cell form lowers the reading in the yellow at 3:00 p.m., while sky effects keep the others up. Ultraviolet shows the effect of increased atmospheric path in the late P.M. A passing cloud or other disturbance interfered with the blue; otherwise the cells are corrected to read the same, as 85 millivolts at 1:00 p.m.

(2) The Macbeth illuminometer. Screens have been used with the Macbeth illuminometer.[1] Those with sharp cut off, such as the

[1] To use the Macbeth illuminometer in this way, two or three standardizations should be made. (a) The energy curve for the light of the standard lamp after passing through each screen should be established. (b) The energy curve for the best June sunlight after passing through each screen, must be established for the locality of use but without the blue absorbing screen supplied with the instrument. Enquiry should be made as to the character of the dark factor-screens and if they are not of truly neutral glass, corrections must be made for any selective absorption, or if only one is used standardization may be made with it in place. In so far as practicable, the intensity of the sunlight reflected from the plate must be reduced by the use of several thicknesses of the screen used over the eye piece, which is readily done in the case of small pieces of gelatin, when the transmission is a power indicated by the number of pieces. Care must be taken to determine whether the second piece gives the same per cent reduction as the first. The law of exponents often holds only for the second, third, etc., thickness applied, due to reflection from the first.

There is no doubt that rough determinations of the quality of light can be made in this way but a number of simple but troublesome operations have to

noviols, yellows, and reds (332) are best as the shorter wave-lengths can be cut out progressively. Glasses or gelatine which transmit only violet blue and green and yellow may be secured (Wratten filters or Eastman Kodak Company filters). These should be put over the eye-piece, so that both the light from the plate and that from the standard lamp are passed through the *same screen*. The standard lamp blue, for example, is measured against the blue from the plate.

b. Photographic methods. In the photographic methods, which have developed especially in connection with the study of ultraviolet, the light is dispersed into wave-lengths by a grating or prism of quartz and projected against a wave-length scale which appears on the negative. Commonly a wedge effect in length of exposure is obtained by a special shutter, so that the upper part of the picture is affected by the thick end of the wedge. The area affected by light takes the form of a curve with intensity at the various wave lengths plotted to a vertical scale as shown in figure 142 (Davis and Walters, 240). Merton (592) secured a wedge effect by sputtering platinum onto a quartz plate. Where the wedge effect is not secured, the density of the plate has to be judged by some other of the methods ordinarily used (see page 344). Within the medium limits, the density of the plate varies directly, and at about the same numerical rate, as the densities expressed in the logarithmic figures used by the United States Bureau of Standards (240).

V. QUANTITATIVE CONTROL OF LIGHT

1. *Artificial light* (188, 270, 429, 607, 703, 704)

The nearest qualitative and quantitative approach to June sunlight in temperate latitude, is the light from the white flaming arc lamp. By varying the amperage and quality of carbons, the light may be so controlled as to give this result. Figure 150 shows the intensity and quality as compared with noon sunlight in Washington, taken with a plain carbon lamp at 10 amperes and a gas-filled tungsten lamp (from Bureau of Standards Technical Paper, No. 168). The figure has been extended to 300, and a curve added showing

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be carried on first. The relation of the yellow of the sun and the lamp may be used as standard for comparing with noon sunlight. The light reflected from the white plate should be examined also, though it probably reflects all wave-lengths.

the effects of three thicknesses of double-strength window glass in cutting out excess ultraviolet dangerous to animals. Crown glass (fig. 146, *C*, p. 349) is ideal for this. The intensity of illumination of a white flaming arc at 25 amperes is about the same as June sunlight.

The daylight (blue) nitrogen-filled Mazda lamps approach noon sunlight or north skylight, but the illumination is not intense. About 7500 meter candles is the usual illumination from 1000-watt lamps. The photographic type is best. As much as 70 per cent of

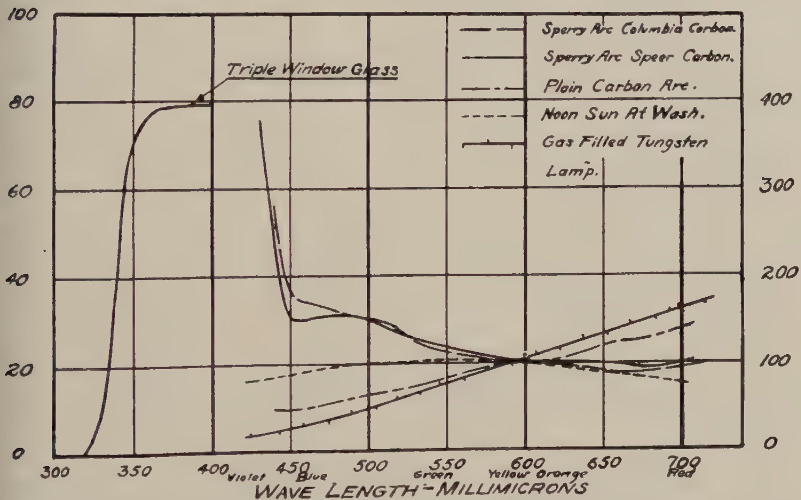


FIG. 150. Showing the relative intensity of different lights at different wave lengths, from Technical Paper 168, United States Bureau of Standards (704) and the short wave length transmission of three thicknesses of double strength window glass by Dr. L. A. Jones of the Eastman Kodak Company. The curves for artificial light are purely relative when 590mμ intensity is given a value of 100 in all.

the energy is screened out by these blue bulbs. The ordinary 1000-watt lamps inside special blue globes usually prove to be more accurate, but the intensity secured is still lower. Priest (701) used two Nicol prisms and a quartz plate to give weak daylight.

It has been found best to mount these lights in a General Electric flood light reflector and direct the light on the cage or object to be illuminated at an angle, 45 degrees from vertical,

2. Maintaining full sun period by supplementing sunlight

At the outset the building should be arranged as shown in figure 162, Chapter XVI.

The difficulties in working with sunlight are as follows: (a) The amount of cloudiness varies from week to week and year to year. (b) The amount of dust and moisture in the air varies. (c) The length of day and the length of atmospheric path vary. The shorter wave lengths, the ultraviolet and blue of the sunlight, are decreased more rapidly as the atmospheric path increases than are the yellow, orange, and red. This means that experiments run in June sunlight cannot be duplicated in August without means of correcting the light differences, a fact particularly important in studies concerning insects with several generations.

For rough work, designed to merely make days of an equal number of hours of light, it has been common practice to expose the plants and animals in such experiments to additional light for a period sufficient to equalize the light exposure period to that of June 21. A rough accomplishment of this is not difficult, but requires considerable equipment. At the University of Illinois the days of uniform length were maintained through several summers by starting on June 22 with a two-minute exposure of white flaming arc after sunset and increasing the length of exposure by the time the sunshine was decreased, that is, about 2 minutes per day. By December 21, the period amounted to six hours. There is no difficulty with the white flaming arc lamps if they are kept in good condition. It is desirable that an attendant be at hand, as occasionally a carbon may come out of the lamp and cause a short circuit which will damage the carbon holders. (This happened once during three years service with two lamps.)

3. Compensation for passing clouds

This was accomplished at the University of Illinois in the summer of 1925 by means of turning on and off lights with the photo-electric cell (503). The lights used were 1000-watt daylight lamps and 2000-watt nitrogen-filled Mazda lamps, though there is no apparent reason why the white flaming arc would not operate successfully. The light switch was made by combining the Kunz photo-electric cell and a modified galvanometer used in the equipment of biological laboratories for turning on fans, closing the circuits to heat coils,

etc. (fig. 151). A galvanometer pointer was substituted for the two-contact metallic thermostat tongue. The two-contact thermostat consists of a bimetallic tongue with a contact point on each side, one to close and one to open some form of heating switch, and is in general use in temperature control. The electric-pneumatic valve formerly used by the Johnson Service Company (fig. 151), in regulating room temperatures has been employed. The valve rotates a lever which opens and closes air ports, through about 30 degrees by means

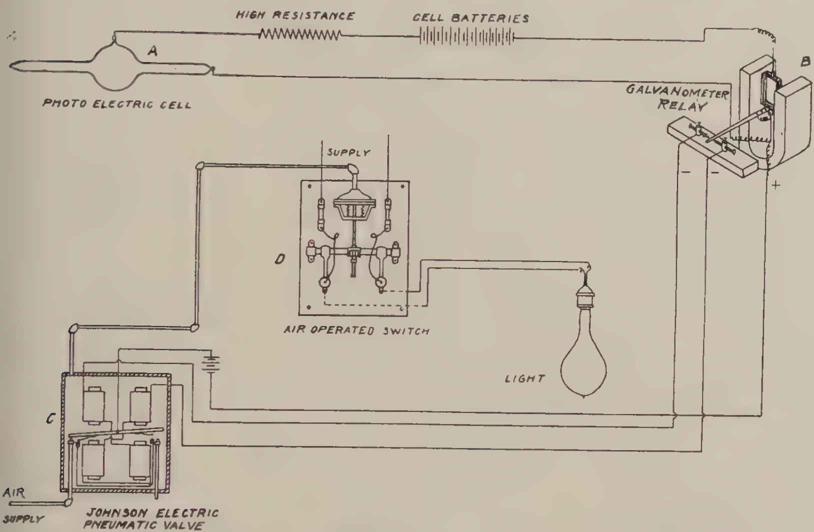


FIG. 151. Diagram of equipment for turning on and off lights (831). *A*, photoelectric cell; *B*, galvanometer relay made from a Leeds and Northrup recorder galvanometer; *D*, Johnson Service Company's pneumatic electric switch; *C*, Johnson Service Company's electric pneumatic valve (*EP*, valve).

of electro-magnets in the bimetallic thermostat circuit. One contact turns on the heat, at the same time opening the circuit on that side and closing the connection with the warm contact. A Leeds & Northrup recorder galvanometer (fig. 151, *B*) was first used by the author to move a hanging crotched wire (in place of the bimetallic sensitive tongue) against the side contacts. This and a later modification of one of these galvanometers in which two small insulated wires passed down in front of the upper-suspension, and to a long pointer, operated a second relay (Johnson electric-pneumatic valve

operated by batteries) in conjunction with a Johnson motor starting switch (fig. 151, *D*) of large capacity and turned on and off lights with large differences in light intensity on a photo-electric cell. The galvanometer proved too sluggish to move the accessories with certainty.

A small General Electric galvanometer relay designed by Kunz was also tried, with success only with the large light differences.

Kunz developed a galvanometer relay with a mercury cup and dipping wire to take the place of the lower suspension (fig. 152). The mercury cup carries a wire to a pointer with a contact on each side,

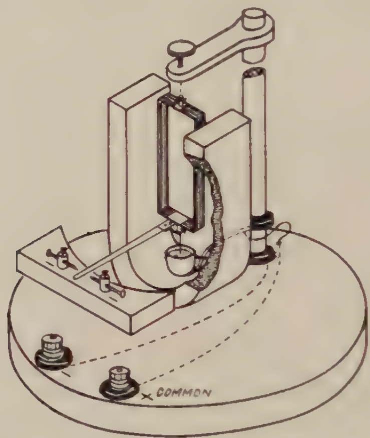


FIG. 152. The essential parts of the mercury cup galvanometer (831). The galvanometer shield is omitted. It supported the hard rubber pieces which held the contact points and screws.

as well as to the galvanometer coil. This operated relay and light switches with differences of 1000 meter candles or less on a photo-electric cell. Much greater sensitivity is possible which assures the operation of switches by very small light differences when a very sensitive galvanometer or amplification is used.

The Leeds & Northrup recorder galvanometer was then modified by connecting the upper end of the lower suspension directly to the pointer (fig. 151).

During the summer of 1925 two photo-electric cells of the ordinary physical laboratory type operated lights for four and one-half months with 100 volts taken from a 110-volt direct current generator, and

with 0.25 megohm Divan resistance units in series (fig. 153). These cells were located in a glass-roofed house where the temperature reached a maximum of 50°C. and remained near 38°C. during much of the day. They were exposed to sunlight which had passed through double-strength window glass, and the voltage remained on them at

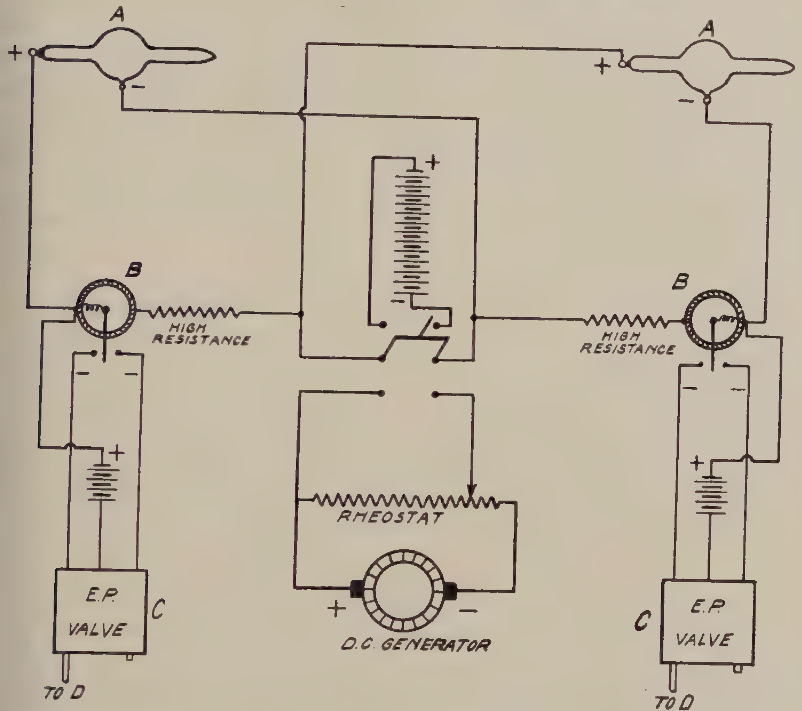


FIG. 153. Diagram of the wiring used in connection with the two complete outfits for turning on lights used in the summer of 1925 (831). The generator and emergency batteries are shown. Other wirings gave trouble which was possibly due to imperfect insulation, but this particular arrangement worked perfectly, even when one cell and one galvanometer operated both *EP* valves and accordingly both lights. For *D*, see fig. 151.

all times. The galvanometers were adjusted so that whenever the sun outside the glass-roofed room gave only dull shadows (as indicated by the eye), the lights went on, and when the shadows became distinct they went off. There was no evidence of deterioration of the cells sufficient to interfere with their operation. The cells were mounted in wire baskets and fastened to a clamp and ring stand,

so that the mechanic in charge could turn the cells two or three times per day to face slightly toward the sun; otherwise, they operated without adjustment for the entire summer period, turning on lights adjacent to chinch bug cages whenever a cloud passed or the sun was dulled.

The two essential features of the apparatus are: (1) The breaking off of the circuit when a contact is made by the pointer. This eliminates the backward swing of the galvanometer due to spark and make-and-break phenomena. (2) The mercury cup which makes possible the use of sensitive galvanometer and the passing of considerable current through the pointer to render the action of the relay sharp and positive. Other methods have been devised but amplification of the cell current is commonly used and adds to the complexity of an otherwise complex equipment.

VI. THE QUALITATIVE MEASUREMENT AND CONTROL OF LIGHT

This is one of the most difficult subjects with which the climatologist and ecologist have to deal. The intensity of various wave lengths varies with the atmospheric path (fig. 142). It is difficult to get an artificial light of high intensity and midday June sunlight quality. There is an important field for careful accurate research, but the equipment required and the expense of doing the work would be very great.

1. The maintenance of natural quality sunlight

Fused quartz is the best transparent substance that can be obtained. It varies in transparency but usually cuts off rather sharply between 200 mμ and 195 mμ, depending on the thickness (Luckiesh (539)). It ordinarily transmits without selection all wave lengths of sunlight. A 2 mm. thickness absorbs almost none of the visible and near ultraviolet. A fused quartz may be secured from the Thermal Syndicate of Brooklyn, New York, in 20 cm. squares at about $100 per square. A cage made of four squares might be necessary to confine small animals out of doors.

The sunlight quality may be maintained for all ordinary purposes by the use of an ultraviolet-transmitting glass (Corning G980A) or other similar glass. The Corning glass transmits 85 per cent at 290 mμ, which is the practical limit for sunlight. The makers of Vitaglass make similar claims for it, though it appears not to have been

studied. Uviol, the Jena ultraviolet glass, is less desirable than Corning. When the angle of incidence is favorable, a roof transmission of 85 per cent is maximal. It is necessary to provide for reflection of light on those units where full sunlight effects are desired. This may be accomplished within the glass-house, or perhaps by the use of special reflecting walls of adjacent laboratories. However, for many organisms full sunlight is not necessary for controls, and full out-of-door intensity is not needed except perhaps for a few experiments.

Various celluloid preparations transmitting ultraviolet have come onto the market recently. They are used in connection with poultry raising. The following two paragraphs have been supplied by Frank W. Jobes, Department of Zoology, Kansas State Agriculture College.

One of these, Cel-o-glass, is made by drying a preparation of cellulose acetate on screenwire. It is patented and manufactured by the Acetol Products Company, Inc., New Brunswick, New Jersey. This product is penetrated to a more or less extent by all the light rays of the visible spectrum and by all the ultraviolet rays down to a length of about 280 mμ. According to the United States Bureau of Standards report on this Cel-o-glass, the maximum transmission of the ultraviolet light is for wave lengths of from 290 to 320 mμ. This range easily includes all the necessary health-giving rays that are contained in the sunlight. The maximum amount of transmission, as given by the above report, is a little above 40 per cent. The Cel-o-glass is very resistant to moisture, wind, and cold, but it deteriorates within the course of some three years when exposed to the extreme heat and excessive sunshine of long summers. The glass is decidedly non-inflammable, although it can be burned. This glass is now being used with seeming success in actual poultry production at the Ohio Experiment Station.

There is on the market a product called Vio-ray glass. This is made by the same process, except that cellulose nitrate is used in place of the cellulose acetate. It is much more inflammable and does not last as long. However, it is much cheaper to produce. The above information was obtained from Dr. ?. S. Houghes of the Chemistry Department, Kansas State Agricultural College. He is planning to publish, in the near future, the results of some experiments and a general discussion of Cel-o-glass in which the above will be given in detail.

2. Experimental variation of the quality of light

a. With sky and sun source. The Thompson Institute has a series of houses with glass-screen roofs, built against the south side of the greenhouse and divided into sections (9 by 11 feet) with opaque par-

titions. The light comes from above. The rooms are kept at the same temperature. The roofs are (1) common glass; (2) ultraviolet giving 85 per cent at 290 mμ and 90 per cent of the other rays; (3) G. 390 Noviol O, which cuts out the violet to 400 mμ; (4) G390 Noviol C, which cuts out the violet and most of the blue to 500; (5) G34, which cuts off all to 540. Results have been obtained (Popp; 682) showing marked effects in plant growth which cannot be ignored with phytophagous animals, no matter what the effects or lack of effects upon the animals themselves may be.

For large animals which can be confined in poultry netting cages, or for those which will not escape readily, the Thompson plan can be utilized. Other smaller animals must be confined in ventilated glass cages, but if such screen roofed rooms are not available ordinary cages with roofs and sides ultraviolet transmitting glass may be used.

b. The supplementing of filtered sunlight. Photo-electric cells and the apparatus for turning on white light may be utilized to turn on colored lights. The cells may be standardized as to color sensitivity. The color sensitivities of cells made from various metals are shown in figure 144.

The methods and equipment described on p. 356 may be used to turn on special lights which pass through ray filters to maintain sunlight at the short atmospheric path value or to maintain a long day or compensate for clouds. For this purpose ray filters over the photo-electric cells are essential. For example, a potassium cell covered with blue glass or a sodium cell in quartz would turn on a white flaming arc as the atmospheric path increased in the late hours of the day. With a suitable blue screen over the light, conditions approximating short atmospheric path quality may be approximated.

A full knowledge of screens and their effect upon light is important. The list, etc., in the Smithsonian Tables (physics) include some that may be made with solution of chemicals (852).

VII. POLARIZED LIGHT

Small beams of polarized light of low intensity can be secured by means of various instruments on the market. A wide beam of polarized light may be secured by means of reflection from a black glass plate. To polarize light, a Corning black glass may be used.[2]

[2] Personal communication from Harry G. Ott, Scientific Director, Spencer Lens Company, Buffalo, N. Y.

The light should be collimated by means of a lens before it is reflected from the plate. The reflection should take place at an angle of incidence of about 57 degrees. This is probably the best method for securing a fairly wide beam of light that is reasonally well polarized. It is not an exact method, as not all of the light is polarized, and it does not give an extremely wide beam.

Experience of the Spencer Lens Co. has been that a beam about 8 cm. in diameter is the maximum for good polarization. The light rays surrounding this 8 cm. center are only partially polarized, and the polarization diminishes rather rapidly as the diameter of the beam is increased.

VIII. THE EQUIPMENT OF LABORATORIES FOR LIGHT WORK

A fully equipped photometry room with various artificial lights, standard lamps, etc., is essential to a research laboratory. Apparatus for standardized lights, for spectral analysis, for standardizing photo-electric cells, etc., must be much more complete and rapid working than is ordinarily found in physical laboratories. Especially the standard lamps must be as large as possible, and ultraviolet sources must be provided and mercury and iron arcs must be available.

In general, photographic methods are not to be encouraged except as checks. All electrometric devices for measurement may be used n control work, thus eliminating plate development work and plate lensity measurement.

Instruments, methods and standards used in spectro-radiometry are discussed by Coblentz (186). In climate simulation it is not necessary to deal with light beyond 280 mμ in the ultraviolet (with fair assurance of covering all the sun's rays); hence some of the difficulty is eliminated. However, it is necessary to be able to detect and eliminate other ultraviolet rays; therefore, quartz and fluorite apparatus must be used. The wave lengths are standardized by means of emission lines from elements as, e.g., calcium, or the well known lines of the mercury vapor or iron arcs. Candle-power standards may be obtained in the form of seasoned incandescent lamps. For radiation standards, seasoned lamps are sometimes compared with a uniformly-heated radiator—the so-called "black body"; but Coblentz recommends that a standardized Hefner lamp or sperm candle be used. The Mazda C gas-filled tungsten lamp of stereopticon type is recommended by Coblentz for the

visible spectrum work. However, it is very desirable to have a larger source to use from time to time in the standardization and checking of photo-electric cells used in sunlight measurement. For this, the 1500 to 2000-watt or more lamp is desirable, and it should preferably be of daylight glass. The gas-filled tungsten lamp is recommended for infrared. As a source of ultraviolet, the mercury arc is rather weak in the sun's ultraviolet region and is discontinuous, but it is probably the most convenient standard available if checked with a thermopile from time to time. Advantage should be taken of its bands in the use of screens. The white flaming arc is not discussed by Coblentz and is hardly suitable as a standard, but it may be used (312a). Manual manipulation of a stereopticon burner to give a constant arc is fairly successful as the difficulties are primarily with the carbon feed. The photo-electric cell may be made especially useful in spectrometry and spectroradiometry.

The use of photo-electric cells demands standardization, especially the testing of ray filters and the wave-length sensitivity of the cells. New cells must be mature and tested with standard lamps of high intensity to determine stability. Test to determine stability must be repeated.

For ecological work a roof observatory space where a large sector disk may be rotated across sunlight is essential and must be so arranged that it may be quickly put into service. Cells should be first tested thoroughly with sunlight, seasoned in light under voltage and finally run with a sector disk under several voltages, e.g., 20, 40, 60, 80, 100 volts. Finally, after all these properties have been worked out, the wave-length sensitivity must be determined. This requires a good quartz spectro-photometer (Hilger) for the ultraviolet. A panel with a movable slit to take the place of the plate holder, so that beams of light of known wave length may be projected onto the sensitive part of the cell, must be carefully made by a mechanician. A thermopile or bolometer with a sensitive part the size and shape of a beam of light must be available. A large dark box with facilities for clamping the cells and racks and pinions so they can be moved in two directions must be available. Both the thermocouple and the cell box must be in a fixed position and on a support so that either the thermocouple or the cell may be brought into position by raising or lowering the box. A duplicate glass spectrophotometer should be placed immediately above the quartz apparatus. This is for the

visible light and is made necessary by the fact that quartz separates the ultraviolet and crowds the visible together while glass spreads out the visible. The *maximum* voltage used with fractional sunlight must be used in all tests to make the results comparable and the sensitivity of the galvanometers must be adjusted accordingly so that there can be a full set of readings at some one voltage.

The development of suitable electrometric apparatus for standardization of cells used in the controlling, continuously measuring, and recording the intensity of radiations of different wave-lengths used in experimental work, and the expression of results in absolute units, cannot be too strongly urged. Otherwise, much valuable work will be doubtful in application and liable to incorrect interpretation. In the construction of laboratories, temporizing in this matter is unprofitable. As the result of not starting right, the natural first step is to develop relative methods, such as the use of photographic plates, which yield data of value but result in blocking the development of electrometric methods.

CHAPTER XV

Evaluation of Factors Other Than Temperature and Moisture, and the Comparison of Species

I. Introduction

For centuries past it has been customary to sum temperature on the basis described on p. 184 (Chapter VII, fig. 73, *B*), with a view to determining the progress of organisms or the causes of their abundance or unusual behavior. This direct use of temperature data, while of value, has failed to produce results of sufficient accuracy in spray calendars, etc. for some years and seasons, especially those in which the animal is most abundant and most erratic in general behavior. In the most successful recent attempt at the direct use of temperature, namely, that of Glenn (338), the temperatures as occurring were extensively corrected to conform to the behavior of the codling moth. If the last century of phenological observation and temperature summing has proven anything it is that direct application of temperature data is to a large degree a failure. This failure on the botanical side is further emphasized by a growing tendency to use plants as indicators (McLean (564), Clements (175, 179, 180), Goldsmith and Weaver). Recent researches have shown that in all cases the response of the organism is the guiding principle.

The consideration of the combined effects of different temperatures and the different humidities which accompany them, is essential, as has been pointed out in Chapter XI, because of their *continuous combined* and correlated action, and the important effects which they have.

Chapter XI is devoted to the development of the equal-velocity chart and to an elaborate method of checking it by the substitution method. All these processes are essential to the establishment of an equal-velocity chart which is similar to table 24, p. 280, but more complete especially with reference to humidity. After such a chart is completely roughed in, it must be tested against actual weather data as described in Chapter XI. One correction most often consists in multiplying the values by a factor such as 1.07 which

represents the difference between the constant temperatures upon which the chart is laid out and the actual variable ones.

Since they vary from hour to hour and there is no certainty as to what humidity will accompany a given temperature, it is necessary to take readings at close intervals or averages over short periods, and the periods or intervals must agree for the two factors.

As has been shown, the average temperature and average humidity for each hour of the day are most desirable for careful experimental or observational work, but under ordinary conditions bi-hourly readings are sufficiently accurate for estimating the amount of progress of life history stages. Either of these methods of reading may be applied to the hygrothermograph tracing or other devices which record at regular intervals on one sheet.

From the detailed readings of hourly average temperature and accompanying average humidity and the completed chart and table of developmental units, hourly velocities may be summed from the hour of the beginning of a stage until the developmental total is reached which is the *theoretical* date of ending the stage. The comparison with the actual date for any individual or series of individuals brings out *individual variation*, and probable *effect of other conditions*, made uncertain or obscured by innumerable fluctuations in temperature and humidity.

The first problem in attempting to discover the effects of rainfall, light, variability, food, wind, etc. under actual weather condition is to evaluate temperature and moisture so completely that the effects of these less regularly correlated factors can be made to stand apart.

Correlation between other environmental factors and deviations from the calculated time for temperature-humidity and average condition of all other factors may be noted and subjected to experimental analysis. In the case of the codling moth the writer succeeded in relating experimental work to actual weather conditions and in establishing temperature-humidity-time developmental units as described in Chapter XI. By means of these units standard theoretical time for the completion of stages was calculated for surrounding conditions of other moths, averaged over several years. Deviation from calculated time was found to be correlated with conditions of other factors. Standard time for the completion of stages is the time in which they should be completed as shown by the developmental units ordinarily required to complete the stage.

Different species may be compared by comparing their tables of *developmental units*. Other (short-cut) methods of comparison are graphic and take into account temperature only. One of these follows the idea of developmental index presented by Sanderson and Peairs (744), elaborated by Powers (685), and utilized in Sanderson's simple form as the "anaesthetic index" by Adams and others (9) in a study of the physiological action of certain organic compounds.

Sanderson and Adams, and others, merely use the reciprocal of time within the straight line limits as the index, but Powers makes corrections for differences in alpha value.

Chapman, who has an especial chapter on this subject in a forthcoming text, uses a modification of this method (157).

II. DEFINITION OF TERMS (826)

It is important at the outset to have the terms necessarily used in mind as they appear in the following discussion. While the writer believes that standard developmental units of the various stages in the development of important pest species should be established, more work is needed to determine whether the standard should be based upon carefully regulated experiments or upon observations of development under natural conditions or upon both. At present variable condition experiments are essential, but the practical adoption of outdoor standards as was done in the case of the codling moth seems most practicable. The variability of stock available for use seems to militate against the establishment of purely laboratory standards. Chapters VII, XI, and XV constitute a unit, leading to the development of these standards suggested in the succeeding paragraphs.

The term *medial temperatures* is applied to that range of temperature within which the increase in rate of development (under constant temperatures) is directly proportional to the rise in temperature. For example, the medial range is about 12° to 24°C. for the codling moth larvae in the apple, and about 17° to 30°C. for all the other stages. It is represented by the straight line limits in figure 72. Medial humidities are the mean range of humidities accompanying medial temperatures under outdoor weather conditions.

Velocity of development is the number of developmental units per hour under any combination of conditions. The reciprocal of time units is relative velocity for any particular case.

The *developmental unit* is the difference in amount of development between that produced in one hour at a given degree (e.g., 20°C.) of medial temperature and the amount produced at the next degree higher (e.g. 21°C. in one hour) as shown by difference in time to complete a stage. It is the degree-hour fraction of total development.

The temperature must be varying at about the rate normal to the average day, because development goes on at a different rate under variable temperature as compared with constant temperature, and other conditions must be average out-of-doors conditions. Hence the *developmental unit* is the amount of development (portion of the total for a given stage of a given organism) produced by one degree of mean medial variable temperature (°C.) operating for one hour in conjunction with a mean medial variable amount of atmospheric moisture, and an average amount of air movement, other factors being average.

The *developmental total* is the number of temperature-humidity-time developmental units required to complete a stage or life cycle. It is not a constant, but varies with the rainfall of a season and the preceding season, with other weather factors, and with the generation and the individual animal.

The *threshold* is the intensity or quantity of any factor just *above* which development begins to be measurable. The threshold temperature is that temperature just above which development begins to be measurable in amount. This is a variable rather than a fixed point and has a statistical rather than an actual value. It differs with the humidity, the preceding rainfall, the individual and the generation. For the codling moth larvae in the apple it is between 6° and 9°C.; for the pupa and the egg between 6.5° and 9.5°C.; and for the hibernated larvae between 6° and 10°C.

Standard theoretical time for a stage is the length of that stage in hours or days as calculated for average organisms from developmental units which take into account temperature and humidity only.

The *substitution quotient* is the sum total of modified and corrected daily temperatures at the time of completion of a stage (see p. 284). The process of determining the substitution quotient, being involved and laborious, is entirely unsuited to practical use though of great value in establishing standards of development and velocity.

The hour and the unit of development as defined above are the fundamental units for estimating progress and predicting time of

appearance. Ordinarily developmental units per hour (velocity) multiplied by the number of hours (time) would be the amount of development accomplished in a given period. However, under weather conditions nearly every hour has a slightly different velocity; hence the time is always one (unity) and the sum total of velocities is the same as the developmental total. The developmental total for any stage is the sum of velocities in units per hour at which development is completed. *Developmental sum* is any sum less than the total.

An *empirical* or *imaginary threshold* is any threshold assumed or calculated which is not approximately correct for the organism in question.

The *hyperbolic zero* is the zero of the equilateral hyperbola (α) to which the time-temperature curve conforms within the medial range of temperature. It is an imaginary threshold.

The *hyperbolic sum of temperatures* is the uncorrected sum above this threshold.

The mathematical relations are simple.

The product of the ordinates and abscissas establishing any point in an equilateral hyperbola is a constant. The reciprocals of the ordinates for the points of the curve multiplied by the constant and plotted on their abscissas give a straight line which crosses the zero and divides the angle between ordinate and abscissa into halves (45°). In the case of velocities at temperatures as commonly plotted, the straight-line portion of the velocity curve makes an angle of 45° with the temperature axis.

From this it follows that the velocity units for any temperature are, in part, of the same numerical value for all organisms having the same α value (hyperbolic threshold). The velocity units at ordinary temperatures for all organisms investigated are of the same order of magnitude, while the *developmental totals vary widely*.

In the course of investigation of the codling moth under the auspices of the Illinois Natural History Survey, numbers of cases were found where there were differences in time while the *alpha* temperature remained the same, indicating that the developmental total is the chief variable.

III. STANDARD LOCALITIES

The standard was developed for the codling moth with material found at Olney, Illinois, 1915, 1916, Olney and Urbana and Plainview,

Illinois, 1917; Urbana, Illinois, 1918, 1919, and 1920. Olney is well located as regards codling moth outbreaks in Illinois. This is not ideal, however, as Illinois is not one of the dense apple-growing centers and only those varieties suited to its climate are grown.

Stocks from great centers of abundance should always be tested and observations carried on at such points. It is not probable that laboratories can be located so as to be in such centers, but some obser-

TABLE 45

Effects of temperature variability, rainfall, etc., on the developmental total of the codling moth (826). The ratios of the developmental totals for 1915, 1916, 1917, at Olney, Illinois, to the average totals for all data are shown.

SPRING PUPAE; RAINFALL, SEPTEMBER TO JANUARY		LARVAE; RAINFALL, CENTIMETERS DURING LARVAL LIFE IN APPLE AND COCOON		PUPAE AND EGGS; — FALLING TEMPERATURE; + RISING TEMPERATURE	
Centimeters	Ratio	Centimeters	Ratio	Week	Ratio
55	0.970	0.0*	0.86	+ fourth	1.08
50	0.980	0.0	0.90	+ third	1.06
45	0.990	5.0	0.93	+ second	1.04
40	1.000	10.0	0.96	+ first	1.02
35	1.003	15.0	0.99	Normal	1.00
30	1.030	16.6	1.00	— first	0.98
25	1.040	20.0	1.02	— second	0.96
		25.0	1.05	— third	0.94
		30.0	1.08	— fourth	0.92
1.00 = 3600		1.00 = 10,000		1.00 = 2146 for egg 1.00 = 3600 for pupa	

* Picked apples.

vations can always be made in the interest of the establishment of a standard value of general application. It was hoped that those for the codling moth could be adjusted by means of locality tables similar to table 45.

IV. FACTORS CAUSING VARIATIONS

The factors (in addition to temperature and humidity) which may cause variation are numerous and are doubtless both internal and external. The former are physiological differences due to past external conditions, and hereditary differences. Hereditary differences have hardly been demonstrated but have frequently been assumed without investigation though the evidence in the economic insect

points to the physiological explanation. Much of the variation in rate, however, is dependent upon variations in external factors operating during the developmental stage in question.

1. Variations correlated with preceding conditions

In the case of the codling moth larvae and pupae, there are differences in the rate of development correlated with the rainfall of the preceding autumn. When the rainfall from September to January is approximately 40 cm. the normal developmental total of 3600 degree (C.) hour units obtains, but the total decreases as the rainfall increases, and *vice versa*, as shown in table 45, columns 1 and 2. The greatest difference shown in this table amounts to 9 per cent.

Stanfuss subjected the eggs of Lepidoptera to high temperature and decreased the average rate of larval development (Henneguy, p. 512) at lower temperatures. The changes in rate produced by moving the organism from one temperature to another for short periods do not belong in this class but the results of Lehenbauer (515), Cook (206), and others showing a length of exposure giving a maximum rate doubtless have a bearing on the effects of variable temperature.

2. Variations correlated with rainfall, food, etc.

There are correlations between the length of codling moth larval period in the apple and the rainfall during the larval life. Since the larvae are entirely protected from contact with the water, and atmospheric humidity, the latter is not taken into account. The units are temperature units only. However, the cause of variation is likely to be food quality, though this may be induced by conditions aside from rain, such as cloudiness which reduces the duration of light. Other examples of the effect of food are cited in Chapter IV. The variations in the developmental total of the larvae as correlated with rainfall are shown in table 45 (columns 3 and 4).

3. Variations correlated with variability of conditions, especially temperature

It has been demonstrated several times that developmental rates are not the same under constant as under variable temperatures. These differences amount to from 5 to 10 per cent (see p. 366). There

re also several other lines of evidence supporting the view that variaility is important. One of these is presented by Huntington (421). 'igure 154, modified from Huntington, shows the survival of persons vhose welfare is influenced by external conditions as related to changes f temperature from day to day. The figure indicates that the differnces may be very great depending upon whether the temperature ises or falls from day to day. Huntington further showed that the fficiency of students is increased by a fall in temperature and ecreased by a rise in temperature (fig. 157) while the efficiency of

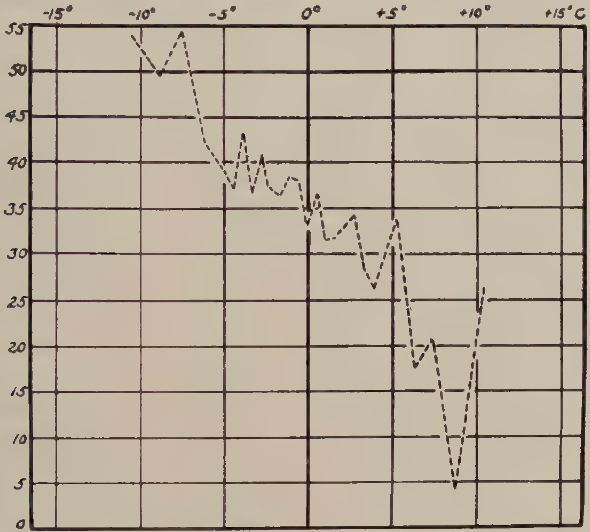


FIG. 154. The survival of the 60 persons out of 120 about to die who may ırvive under the most favorable weather conditions or who may die under the ost unfavorable as affected by rising or falling temperatures from day to day 119).

orking men is improved by a change in either direction. In all ases continuation at the same temperature from day to day is not imulating. Davidson (239) has shown that falling temperatures inrease the total solids and per cent of butterfat in cow's milk (figs. 55 and 156).

In the case of the codling moth the length of the life history stages influenced by rising and falling temperatures. The effects are best easured in weeks and, as shown in table 45 (columns 5 and 6), may ary as much as 16 per cent depending upon whether the temperature

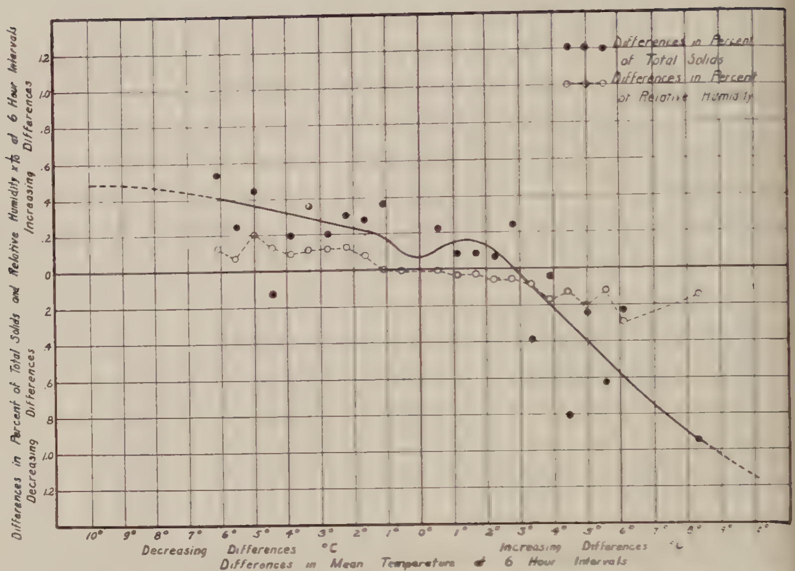


FIG. 155. Total solids of cow's milk in relation to rising and falling temperature (239).

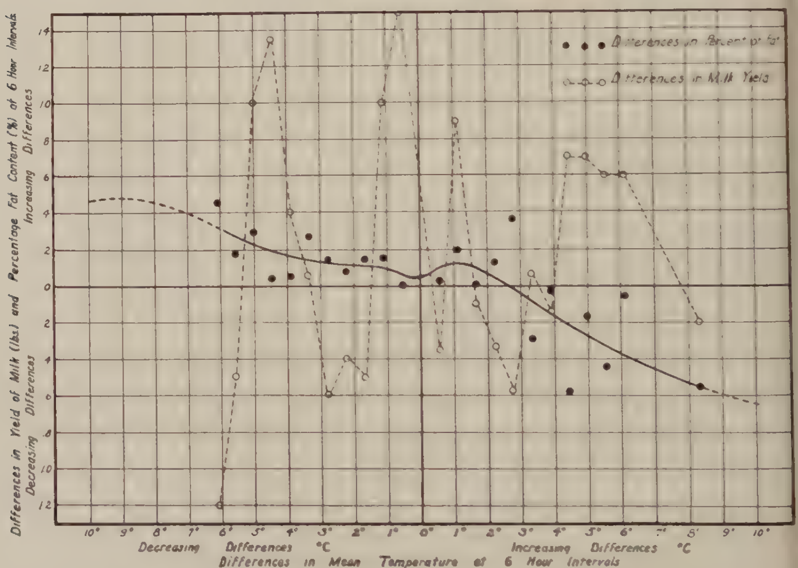


FIG. 156. The butter fat relation (239)

rises or falls from day to day. This type of effect is further well illustrated in figure 158 in which the substitution quotients of codling moth pupae are plotted on the center of the pupal period as shown by a line the ends of which are immediately above the dates of pupation and emergence on the scale below. The correlation with the upward and downward trend of temperature is quite striking. The actual demonstration that temperature rise and fall are the cause, awaits experimentation. With "Thermotyme" thermostats this could be worked out.

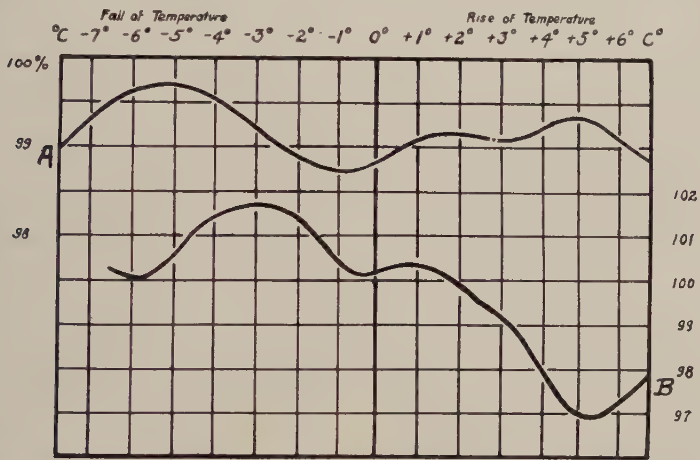


FIG. 157. Efficiency of working]men (*A*) and of student's (*B*) with rising and falling temperatures (421).

4. Variation due to internal causes

That any set of variations is due to hereditary causes is to be proved and not assumed. Possibility of analysis through breeding is suggested by the stringing out of pupations in the codling moth larvae that have been subjected to the same conditions and collected on different dates. This phenomenon is illustrated by figure 159.

V. THE RELATION OF ABUNDANCE OF INSECT PARASITES TO WEATHER CONDITIONS

1. General considerations

One often thinks of insect parasites as governed by different and more intricate laws or rules than other organisms. This is not, how-

ever, especially true of insects parasitic on other insects. In the main they are similar to insects feeding in the bodies of plants or on dead animals. As to causes and factors covering abundance, little appears to be known, and it is the purpose here to indicate some of the general types of methods which will probably prove helpful in the investigation of the question.

Granting a sufficient number of individuals of the one or several host species, the abundance of a parasite is controlled primarily by the following: (1) Survival during adverse periods or periods of inactivity.

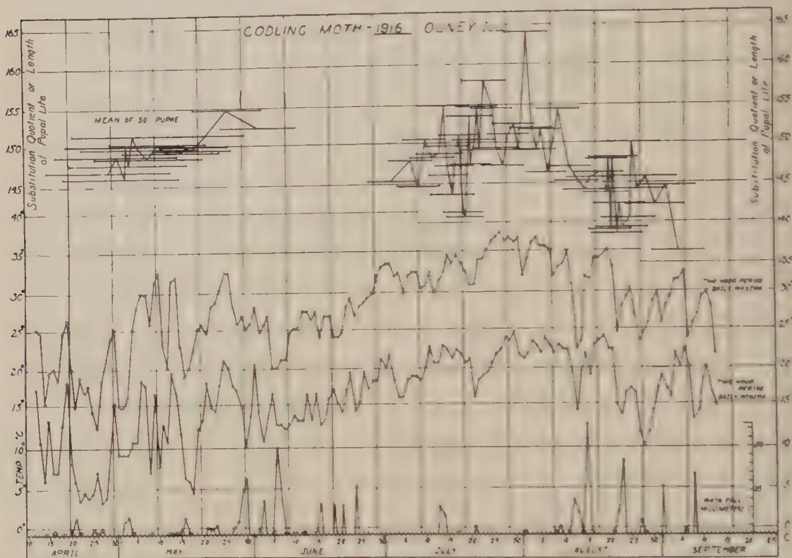


FIG. 158. Showing the increase in length of pupal life of the codling moth with rising, and decrease with falling, temperature. The curve is drawn through mid-pupal life.

(2) Rate and duration of development of new generations. (3) Activities controlling fertilization, egg laying, migration from host to host, etc.

2. Survival

There is nearly always more or less mortality during periods of inactivity. After a period of hibernation, aestivation, or cessation of activity, the number of surviving parasites is determined or is markedly affected by weather and climate and is of interest in relation to

the survival of the host. In this regard evidently no definite rule can be laid down as to conditions suitable for the survival of parasite and host during rest periods. Weese (960), who studied the large orb weaving spider (*Epeira gibberosa* Hentz) and its egg parasite

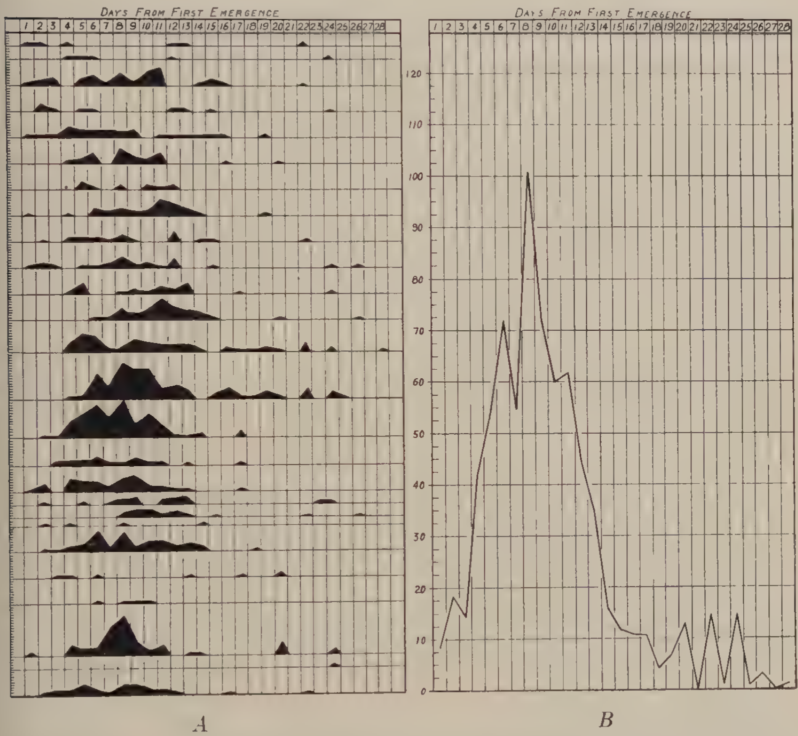


Fig. 159. Part *A* shows the order of emergence of moths beginning on May 3, which is number 1 of the top scale, and continuing for 28 days; the close scale at the left indicates number of individuals emerging each day in each set. The treatment of the larvae and the date of collection of each set is indicated in 826.

Curve *B* represents the sum of all emergences shown in Part A. This curve shows three groups commonly recognizable in pupations out of doors, viz., a small group at two days, a very large one with its maximum at eight days, and a somewhat drawn-out group beginning at twenty. Cf. Glenn's Charts 1, 2, and 3, noting pupation (338).

(*Arachnophaga picea* Riley) during hibernation, makes the following statement:

It was evident that the hymenopterous insect parasitic on the eggs of this species (*Arachnophaga picea* Riley) was able to reach maturity and to emerge

under much more varied conditions than those favorable for the development and emergence of the spiders.

Likewise Hefley (382), working on a tachnid fly (*Wintheuria 4-pustulata* Fab.) parasitic on the tomato worm, found that the host was much more sensitive to a large amount of moisture than the parasite. Unparasitized host larvae suffered from fungus diseases. The parasites emerged, however, from fungusized host larvae. Dry soil was detrimental to both.

Lysiphlebus tritici, a parasite of *Toxoptera graminum*, passes the winter only in the pupal stage (Glenn, 417): all larvae are killed when the host is killed by cold weather. The host passes the cold winters in the egg stage, thus reducing the hazards and probably giving the host advantage. The chinch bug egg insect parasite hibernates probably as a pupa in an egg (not common in autumn) or as an adult, which would again be of advantage to the host which hibernates in numbers in the adult stage. Many other cases could be cited showing that, in one case, there are indications of advantage to the insect parasite and, in another, to the host. No definite rule can probably be laid down.

3. Rate and duration of development of new generations

The number of parasites surviving an adverse period is the basis upon which all increments must be built. Here again the number of parasites is of especial interest in comparison with the abundance of a host insect and hence is measurable in terms of a host or of its effect upon a host insect. Abundance of parasites in a given season granting an average number of survivors from a preceding season is governed by: (1) Rate of development to maturity (the length of time between generations). (2) Duration of reproductive life. (3) Rate of reproduction during reproductive life.

These rates and durations are influenced by weather. In considering the effects of weather factors, all attempts at direct application of weather data must be abandoned. In this type of study as in those already described, chief reliance must be placed upon the behavior of the organism in question under conditions which may be regarded as standard, as already described.

The work of Headlee (380), Glenn and others on the grain aphis (*Toxoptera graminum* Rodeni) and its parasite (*Lysiphlebus tritici* Ash) makes possible a comparison of the life relations of these two

species so as to illustrate the principles outlined above. The curves are not, however, presumably correct, and the developmental totals, thresholds, etc., are only approximate. It is possible to determine the relative rate of development from curves of reciprocals of time under constant temperature or variation within limited ranges. Thus in figure 160 the curves of the host and parasite are drawn from

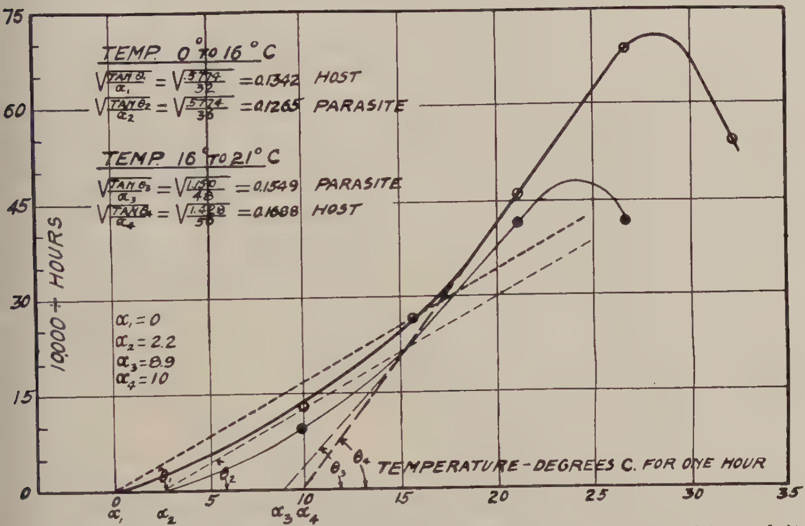


FIG. 160. The velocity of development curves of the grain aphis and its parasite after Headlee (380). The circles indicate his data. The curves are 10,000 times the reciprocals of time. Any point read from one of these curves on a particular temperature divided into 10,000 gives the time required to complete a stage. The basis on which these curves are drawn is evidently not in accord with the characteristics of organisms. The method is however useful in estimating the relative rate on the basis of the value of α and the tangent of the angle θ as shown in the figures. Both approximations show that the rate of development is highest in the host. Between 0° and 16°C. the host velocity is 0.134 and the parasite 0.125, while between 16°C. and 21°C. the host is 0.168, the parasite 0.1549, the host being the faster.

Headlee's data as best they could be. (The curve of the parasite is adapted to a single point in the medial temperature limits and does not purport to be more than approximate, but it is suitable for illustrating the method.) The lower the threshold, the more rapid is development at any point above it; hence, the rate of development varies inversely with alpha. The steeper the curve, the more rapid

is development; hence, $\frac{\text{Tan } \Theta}{\alpha}$ is the product of the two, and this mean effect is $\sqrt{\frac{\text{Tan } \Theta}{\alpha}}$. An inspection of fig. 160 shows that the host develops faster within both ranges of temperature approximated by the dotted lines which give rough expression to the curve.

Figure 161 shows the velocity curves in units per hour for three

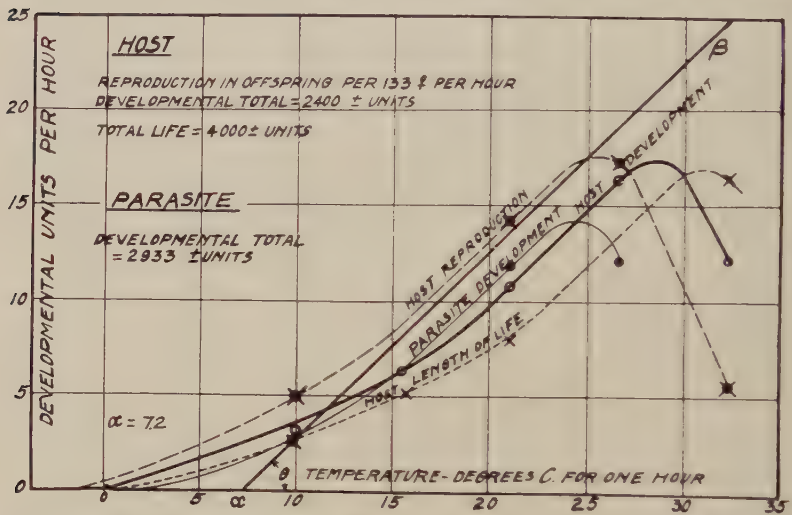


FIG. 161. The data of Headlee (380) covering rate of reproduction and length of life as well as rate of development for the host and parasite. Drawn with reference to their different natural constants and in accord with the idea of a constant sum total for metabolism; the thresholds are estimated from the observations of Glenn. The height of these curves may be read off on the developmental unit scale and divided into the constant to give time for completion of the process in question at a particular temperature. The difference in length of developmental periods is brought out here by the difference in constants. The developmental units do not differ greatly for the different organisms or stages at the same temperature. The β line shows the velocity that would be assumed in summing temperature.

aspects of the life of the grain aphis as the host and *Lysiphlebus* as its parasite. It will be noted that the three curves for the host rise in a concave curve from the threshold, then rise in a straight line through a few degrees (medial temperatures), and then turn downward. This form for the curves could not be ascertained in detail from the data of Headlee. They were given the general form characteristic of such curves on the basis of the data of these investigators. The curves for

he host in particular are straight for only a very short temperature nterval. The straight-line portion is well indicated by Headlee's onstant temperature experiments. The thresholds were determined hiefly by Glenn during the outbreak of 1907–1908. The rate of de- elopment of the host under ordinary variable temperatures is on the vhole slower than that of the parasite, but the velocity is high for the ıost above 24°C. while it is much lower for the parasite. The thresh- ıld for the host is 0°C. while that of the parasite is 2.2°C. The de- elopmental total of the host is 2400(°C.) units while that of the ıarasite is 2933(°C.), and the units are of the same numerical value. At a mean temperature of 20° (with variation within the medial ange) a parasite would develop in 264 hours; a host would develop n 240 hours. While the parasite was developing, the host would ıave produced 26.4 individuals. The parasite would ordinarily ting 22 aphids during the two days following its emergence, when he total produced by one female would be 31.2 individuals, this be- ng 9 individuals ahead of the parasite. It alone could then never xterminate the host. It is easy to see how important a little delay n the progress of one species may be in determining the abundance f either a little later.

4. *Controlling activities*

Attention has recently been drawn to the importance of faint light ı conjunction with certain temperatures in controlling the egg laying f the codling moth. Isely and Ackerman (428) believe that this may ontrol the abundance of the moth.

Some parasitic insects are similar. Glenn states that *Lysiphlebus* oes not sting the grain aphis in cloudy weather but remains inactive nd in hiding, and that meanwhile the aphis continues reproduction. IcCulloch and Yuasa (561), on the other hand, find that the insect arasite of the chinch bug egg lays eggs at all times of the day or night ı either light or darkness.

VI. INDISPENSABLE OBSERVATIONS

The final test of abundance and its causes is *abundance* itself as orrelated with weather conditions. This means continuous obser- ation of parasites and other insects by means of weekly or daily uantitative collection throughout many years. All other animals ıould, so far as possible, be included in the collections. Some will

serve as indicators of the abundance of other important species. This means a procedure similar to that in common use in the study of aquatic organisms. Such observations overshadow experiments in importance, but experiments are still necessary to determine which of several correlated factors are in control in each case. With a century of observations, most problems might be illuminated, but experiments may readily make ten years work equally valuable.

VII. BIOTIC POTENTIAL

Chapman (157) (see also Chapter II) has discussed what he calls biotic autecology. Under this heading he discusses *biotic potential* which is concerned chiefly with the rate of reproduction (reproductive potential), survival (survival potential), power to synthesize food (nutritive potential), and protective reactions and structures (protective potential). Operating against the various potentials is the *environmental resistance.* He states that biotic potential is a quantitative expression of the dynamic power of the species which is pitted against the resistance of the environment. Formulae are presented for calculating the number of individuals when the biotic potential and environmental resistance are known or of finding mathematical expressions for environmental resistance when the biotic potential and population are known. The calculations obviously become complicated and have as yet been applied to only a few simple or theoretical cases. The principal value of such a suggestion lies in the fact that it will probably stimulate study of fecundity and survival of various animals. It will be unfortunate, however, if these are not chosen from the predominants whose behavior is of prime importance in synecology.

CHAPTER XVI

The Location and Planning of Buildings and Equipment for Climate Simulation

I. INTRODUCTION

In the first six chapters of this book attention was focussed on the general climatic and biotic relations of communities and their predominant species. The content of Chapters I and II emphasizes the importance of biotic and climatic observation in relation to experimental work in, and out of, the laboratory. The other preceding chapters emphasize the effect, measurement, and control of various single factors and combinations of two or three factors. It is the purpose of this chapter to suggest the general principles governing the location and designing of buildings, equipment, gardens and natural areas which will make possible the control of a maximum number of conditions both in the field and in the laboratory.

The most neglected factor and, at the present time, the most difficult one to control and measure, is light. Since the length of the day and the quality and the intensity of light influence animals directly and also indirectly through effects on the food (Chapters IV and V), this is one of the first considerations in the planning of buildings. These facts are further emphasized by the grave difficulties in the way of detailed measurement and control of light. These difficulties are increased because of the uncertainty of the quality of artificial light and the cost of producing it in an intensity equal to that of sunlight. The cost of illuminating a small area in this way may easily amount to from fifty cents to a dollar per hour. Every effort should be made to utilize all possible sunlight throughout the day. To accomplish this all astronomical facts bearing on the question must be considered. Roofs must be constructed so as to receive and transmit a maximum amount of light. It is easy to shut out light if it is not wanted, but very difficult to supply it in an ordinary building if it is wanted.

Attention has already been called to methods of controlling temperature, moisture, light, air circulation, etc. Temperature control

involves heat sources, running water, refrigeration, circulating devices, and automatic control. Humidity control requires all that heat control does, and special equipment in addition. The two go hand in hand. Light control likewise involves temperature and humidity relations. Air movement influences evaporation and hence temperature and humidity. A particular condition of a single factor, as commonly operating, is accompanied by certain conditions of various other factors. Unfortunately the condition of the other factors has too often not been stated; e.g., in experiments under constant temperature which are of necessity accompanied by certain humidity conditions. If experiments are made with several constant temperatures, the humidity should either be held the same or shifted to a position which is average for the habitat of the species being tested and for the temperature (Chapter XI). In climate simulation work a large series of combinations of several factors is necessary. Their simultaneous operation is also important (see p. 276). The present chapter is concerned with combinations of the ideas and methods suggested in the preceding chapters. The primary purpose of climate simulation laboratory facilities is to accomplish two things: (a) To actually simulate idealized or simplified days for a certain climate or season: and (b) to maintain, for a considerable period, a constant combination of climatic factors known to occur in the habitat of the species under consideration, in the course of daily and seasonal fluctuations. It is also highly desirable (c) to breed animals continuously over a few seasons under modified climate to ascertain the effect upon the abundance and general success of the species used. It is often quite important (d) to give more careful and critical attention to quiescent periods than to active ones. Gardens and grounds where these types of experimentation are to be carried on should be planned with a view to all the factors involved.

II. GENERAL LOCATION

The laboratory should be located where the problems to be investigated can be checked out-of-doors in the climate where the species involved occurs. If agricultural pests are to be investigated, an agricultural region is to be preferred, but nearness to *natural* areas is also important, because of the value of the native biota as an indicator of climatic fluctuations.

Because of the diversified problems in North America there should pe a number of laboratories in different localities. The problems of orestry, grazing, and agriculture demand a background of experinental work. The results are unfortunately too long in being acquired to appeal to the government agencies in charge, and laboraories should be privately endowed to pursue their work with least hindrance from the standpoint of immediate application.

The laboratories must be located in the country where there is plenty of space free from buildings and trees, and where buildings can be arranged so as to give full lighting.

Many of the state and provincial agricultural colleges are adnirably located and with ample grounds for the proper arrangement of buildings. If the plan is correct at the beginning, a very desirable plant may be built up in small sections.

III. GENERAL FACILITIES

In planning general laboratory facilities it appears to be customary for an interested person to go to as many laboratories as possible and bring back ideas to be incorporated in the plan for the building and equipment. Such a method is good provided the visiting person lays aside his notes and forgets them until a correct fundamental plan has been arrived at. The reason for this is that most laboratories are mere buildings and "greenhouses," not at all modern from the standpoint of animal response requirements. They are usually so badly constructed as to light and temperature control as to put them entirely out of consideration. The problem must be studied from the standpoint of the sun's azimuths, elevations (913, 914), and intensity at different times of the year, and with reference to surrounding objects likely to interfere with lighting. The topography, prevailing winds, etc., and plan for the arrangements of the building accordingly should then be considered. In the construction of glass houses, the traditional plans for commercial greenhouses, which can be purchased ready to be assembled, must be abandoned altogether. The glass houses needed in experimental biological work are *not* greenhouses and should not be so regarded at all. The traditional gardener who is always at hand ready to adjust ventilators and steam valves is not ordinarily a reality. The fullest equipment of automatic devices should be utilized. The architectural style adopted by the institution must not be allowed to interfere with producing an adequate building.

Building and garden facilities meeting the requirements of modern ecological and climatological work have not, to our knowledge, been provided for in animal work anywhere. Such plans as have been executed have taken into consideration only a limited number of problems concerned with the control of conditions. Three matters, namely, lighting, control or reduction of midday high temperatures in glass-roofed houses, and provision for outdoor controls and experiments, have been almost entirely ignored. This has grown out of the fact that biologists, in an attempt to analyze the internal mechanism of organisms, have imitated physicists and chemists in their use of constant-temperature equipment in darkness. The concept of these analysts seems to have been that the organism is a much simpler mechanism than it is now possible to consider it to be. In general, their experiments were badly controlled, and had not some of them possessed special ability to draw good conclusions from bad experiments, progress would have been slow indeed. *Variability*, so very important to most organisms native in temperate regions was ignored; the sun's ultraviolet, now known to be very important, was screened out, even in climate-simulation work. The idea that the natural environment is so complicated that it is impossible to analyze it, furthered these tendencies. They were especially favored by the emphasis placed upon *evolution* and the insidious Weismannian doctrine of the insulation of the germplasm from the environment.

In planning facilities it is necessary to make a full survey of the astronomical phenomena concerned with the light from the sun and moon, its relative intensity from time to time, the shadows cast, etc. If not planned rightly from the beginning, very elaborate plants may become essentially useless for general purposes, because of the improper arrangement of buildings and grounds.

1. General plans for buildings and grounds (217, 249, 913, 914)

It is very essential that the plan for a plant in which climate simulation is to be carried on be very carefully considered. Light is such an important factor that no building should be located near enough to the glass-roofed houses to cast a shadow over an essential part of their contents. If a building is to be located to the north, its distance from the glass-roofed houses is determined by the latitude. The sun crosses to the north of a parallel of latitude on which the building stands at a fairly early hour in the afternoon, at certain

seasons, and does not come into a due east position until rather late in the morning. The exact extremes have to be determined from the latitude at which the laboratory is to be built. For example, at 50 north latitude the sun rises nearly $37\frac{1}{2}$ degrees north of due east on June 21 and does not cross over the due east line until two hours after sunrise. It crosses back again about two hours before sunset. Thus, any glass-roofed house immediately south of an ordinary building will have its northern edge in shadow for four hours on this date and for a lesser time—decreasing for the three months following and increasing from zero to the maximum during the three months preceding. At 40 degrees north latitude the same principle applies but the maximum is 30 degrees and the total time that the sun is north of a due east line is increased to nearly seven hours for the day (913, 914). At 30 degrees the maximum is 27 degrees north and the maximum period of shadow is eight hours.

Figure 162 shows a plan for a climate simulating laboratory at 50 degrees north latitude. The ground plan shows glass-roofed houses 200 meters (660 feet) long, so arranged that the building north of them will not cast a shadow in the morning or afternoon. This is most effectively brought about by turning a corner of the building to the south. Two wings extend northwest and northeast to make a V. The glass-roofed house must be a single row as in figure 162A or the more southerly units will shade the northerly ones in the early and late hours of the day in winter.

If the glass-roofed houses are arranged with long axes from north to south, the outer houses will shade the inner or central ones. If they are arranged with long axes from east to west the more southerly ones will shade the more northerly, especially in winter. This difficulty may be limited by placing those likely to be shaded in winter on a higher level (fig. 162B), which causes early morning and evening shadows in summer. Differences in level are not difficult since basements are necessary to the building. As will be shown later, houses with axes east and west will probably prove less troublesome if the roof is especially constructed. These, accordingly, will be discussed from the point of view of shadows from the south especially in the winter, due to the low angle of the sun. At 50 degrees north latitude its zenith distance is $73\frac{1}{2}$ degrees at noon on December 21. This is the period of shortest days, and shadows should not be allowed to fall upon glass-roofed houses. To prevent

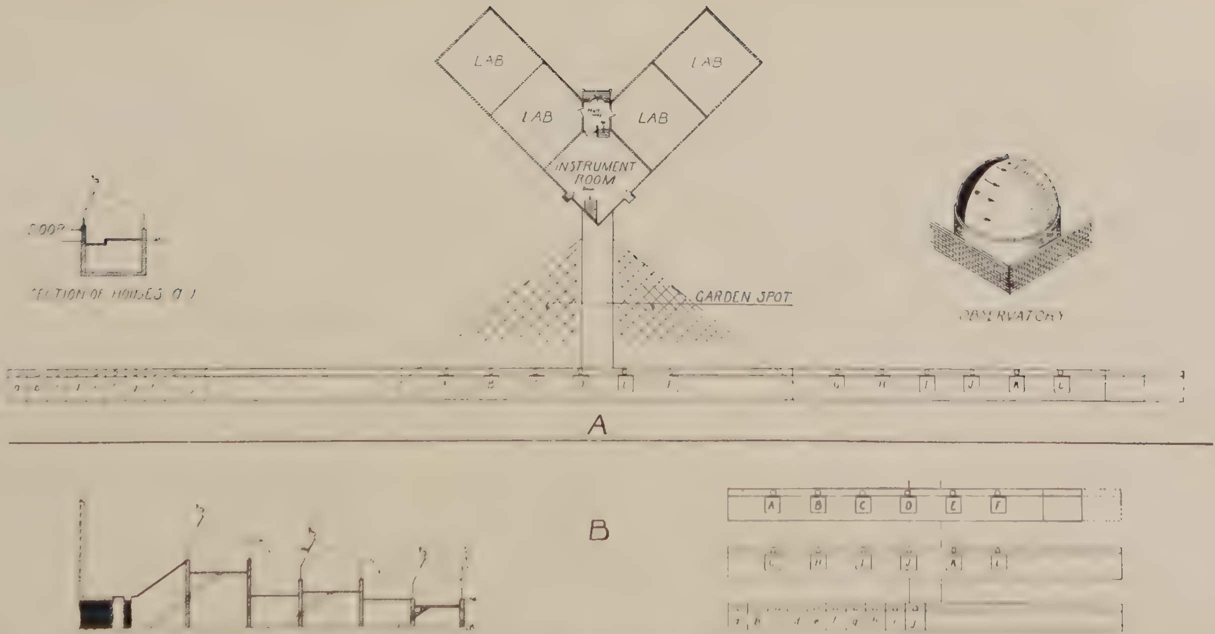


FIG. 162. *A* shows an ideal layout for an experimental laboratory with glasshouses. This position of laboratory building is desirable to enable the sun to reach only the center section glasshouse at all times. The broken lines running from the corner of the building show the limiting border of the building's shadow. The distance between the laboratory and glasshouse would have to be increased to put all in the sun. The crosshatched space would be suitable for garden experiments as it is shaded very little. At the right end of the glasshouse is a section with a movable roof; the roof operates on rollers and may be moved outward to uncover the section. On the left end of the glasshouse are 10 sections (*a–j*) which are roofed with different kinds of glass to pass different rays of light. These sections are provided with door and flooring as shown in detail, to enable one to put a large animal in the house for experimental purposes, such as effect of light rays on milk. *A* to *L* show location of units shown in figure 166. On the roof of the main building over the instrument room is located an observatory as shown in detail. This is necessary to carry on experiments on light.

B, another glasshouse layout not as favorable as in *A*. Three sections, located one behind the other, are terraced

his it is necessary to make the more southerly houses lower than the others, but even then they will cast a shadow early in the morning.

Figure 162B shows a plan for a glass-roofed house at 50 degrees north latitude. This may be used when the plan shown in figure 162A can not be used from lack of ground space. The houses are so arranged that they will not cast a shadow on each other on December 21 at noon. An angle of 73 degrees over the peak of one strikes the other below the glass line. Figure 162B shows a plan for a building to the north of laboratories which cast shadows.

2. Construction of the glass-house roofs

The ordinary greenhouse construction calls for a rather wide wood or metal area at the peak, particularly if there are peak ventilators. Peak ventilators also involve a wide opaque area at the lower edge of the ventilator sash. If the peak of such a greenhouse extends north and south, it causes rather wide shadows, which pass progressively across the room below from morning to afternoon. They may keep a poorly placed small animal cage in the shade for a considerable period of time. If the long axis of the greenhouse is east and west, the shadow cast by the peak will fall on a particular point during a good part of the day over a considerable period at some season of the year. For example, a particular animal cage may be partly in shadow for a good part of a month. On the whole, however, the advantage is all on the side of the glasshouse with the axis from east to west. There are certain parts in which equipment may be set up and not come into shadow at any time. By making the roof asymmetrical and moving the peak to the north of the center, practically the entire space may be made available without shadow after an early morning hour in summer. The second advantage in this arrangement will be indicated in connection with the enclosed units.

3. Roof materials

If possible, some kind of ultraviolet-transmitting glass should be used in glass-roofed laboratories. In such buildings there is always a loss of light because of smoke and dust on the glass as well as through reflection. Even if the roof were sheet quartz, there would be a considerable loss of energy. Accordingly, the light reaching the animals and plants under the glass-roof is always less than that

outside. There are two practicable means of bringing the radiant energy level up to the approximate normal. One consists in making the south wall of the building which is to the north of the glass-roofed houses of some material which reflects radiant energy. Glazed white bricks reflect considerable light, but whether they reflect ultraviolet has not been ascertained. The second possible method is to have the roof and frame of one glass-roofed house so arranged that it can

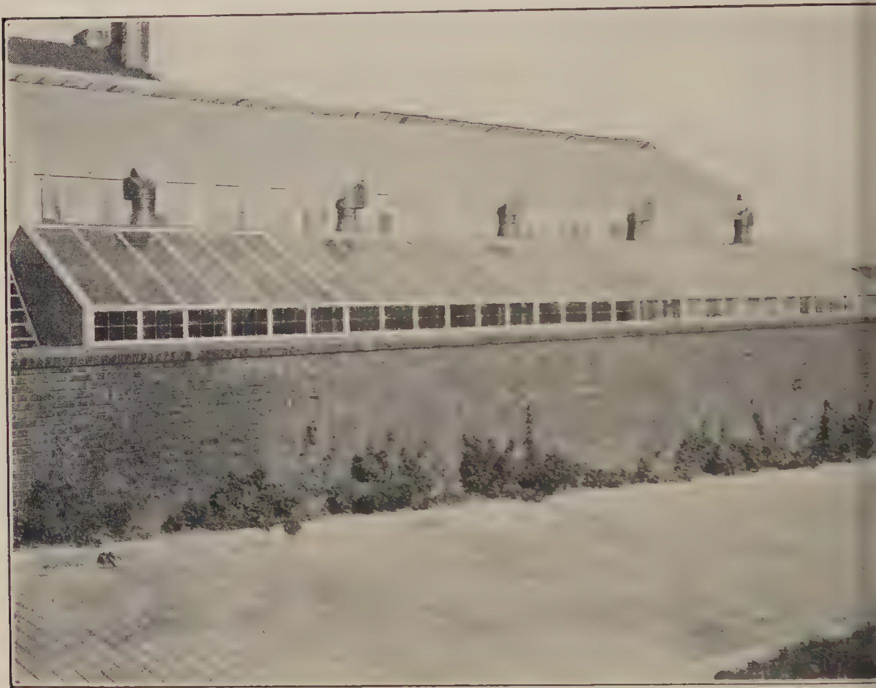


FIG. 163. Thompson Institute glasshouse showing south facing rayfilter roofed sections (after Popp, (682)).

be rolled from above the house on the track of rollers. At the Thompson Institute such a framework and track is used to bring electric light above certain of the glasshouses during the night. The lights are mounted in the top of a large steel frame which may be rolled out of a shed and over the glasshouse at will. Such an arrangement could equally well be made to remove the entire roof of a section of glasshouse whenever a storm was not actually in progress,

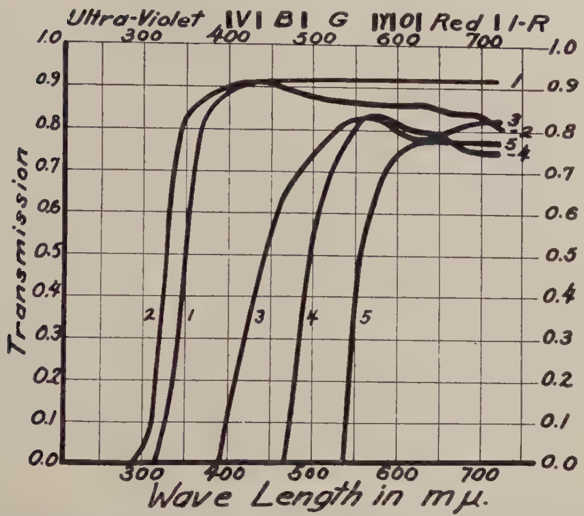


FIG. 164. Showing the transmission of the rayfilters in the house shown in Fig. 163 (after Popp (682), courtesy Boyce Thompson Institute) (see p. 138).

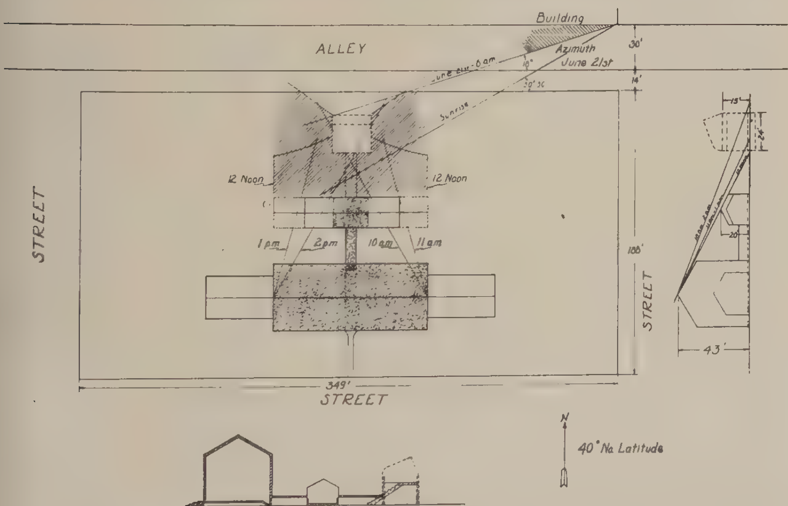


FIG. 165. Ground plan of the University of Illinois Vivarium. With badly lighted glass roof units at the east and west ends of permanent structure. With a proposed second story light laboratory shown to the north. The elevation is shown below. At the right the full lighting is indicated for December 21. In the upper right hand corner the sun's azimuth subtracted from 90° is shown for sun rise on June 21. The building throws the site into shadow until 6:00 a.m.

during the day in summer. This would have the advantage of preventing the temperature from rising to a high point. We are not, however, aware that either of these plans has been put into practice.

4. *Glasshouse basements and air conditioning*

Glass-roofed houses should be conditioned so as to prevent the midday temperatures rising above those occurring outside. Basements are needed for the ducts which must be used to suck or force air through the glass-roofed rooms. The basement space is also very useful for storage of rough materials such as soil, fertilizer, and rough equipment such as pots, benches, etc. This is a very important departure from the usual construction.

IV. APPARATUS (873)

1. *Methods of building and caring for apparatus* (470)

Methods of constructing apparatus have not been managed economically. At the outset engineers who have specialized in this field have rarely been available, and laboratory directors have rarely had the idea that the organism dictates the character of the equipment and have permitted purely mechanical ideas to dominate. More often a lack of funds for the project has made it impossible to let a contract to a responsible firm and have the job completed. Where a mechanic or caretaker is employed he is usually given the job of completing or building the desired units. Materials are drawn from store rooms, time is expended to experiment on the project, and the expense frequently exceeds the completion cost of a much more satisfactory unit installed by experts, provided they are available.

The attitude of the investigator is commonly wrong either because of necessity or training and traditions; he makes his apparatus *simple*, so that his time may be devoted to the investigations instead of the running of the apparatus. This is correct where simplicity is possible, and should always be in mind. Most climate simulation work, however, is not simple, and the apparatus can not be made simple. The proper thing is to make estimates and plans for help accordingly.

2. *Climate simulation units*

a. Units for small animals. The units here described will be useful for animals up to the size of poultry and rabbits. Such climate

imulation units should be arranged in a glass-roofed building as hown in diagram figure 162A, which provides for seven rooms, pproximately 3-meter cubes (*A* to *G*) with temperatures ranging rom 10° to 40°C. The glass-roofed house in which the temperature nust be held at outside air temperature or below, at the midday naximum, by means of air conditioning apparatus, encloses them.

It *is ordinarily necessary* to run experiments at each of *seven emperatures.* Four or five humidities at least must be available in ach unit. These units should be arranged some distance apart, o that they may secure the maximum amount of light on all sides. Plans for holding the temperature of these units constant are shown n figure 166 as prepared by Mr. D. C. Lindsay, of the Carrier Engineering Corporation of Newark, New Jersey. The air is heated or cooled and forced into the room at a rate necessary to maintain he temperature required. There is no provision here for controlling he humidity of the air. Steam and cold water or brine coils are provided for cooling the air or warming it as necessity may demand. The air coming into the room passes over the cooling coil or over the heat coil or both, depending upon the position of the damper. The hermostat operates a direct-acting valve that opens and turns on the steam at the same time that a reverse acting valve turns off the cold water. The second thermostat is located in the room outside, and whenever the room temperature is higher than is desired for the special chamber, the steam is turned off and cold water is turned on and the dampers are set to turn the air over the cooling pipes. The chamber so cooled is an 8-foot cube (fig. 166) with a shelf at standing table height and 18 inches wide around the inside except for a door at the north (fig. 166). The temperature of the room may be kept constant by such a method. It is the opinion of Mr. Lindsay that these units would be no more expensive than the materially less effective ones to be described later in this chapter. The roof of the glasshouse in which such units are located and of the units and other containers should be made of some single thickness ultraviolet-transmitting glass. Three thicknesses will materially reduce radiation in any event even if the glasses are kept scrupulously clean. The question of using the roof of the glasshouse as the roof of the units should be considered, but without some special arrangements this is quite sure to cause the different units to be unequally illuminated.

For small animals there must be small cages with a minimum of

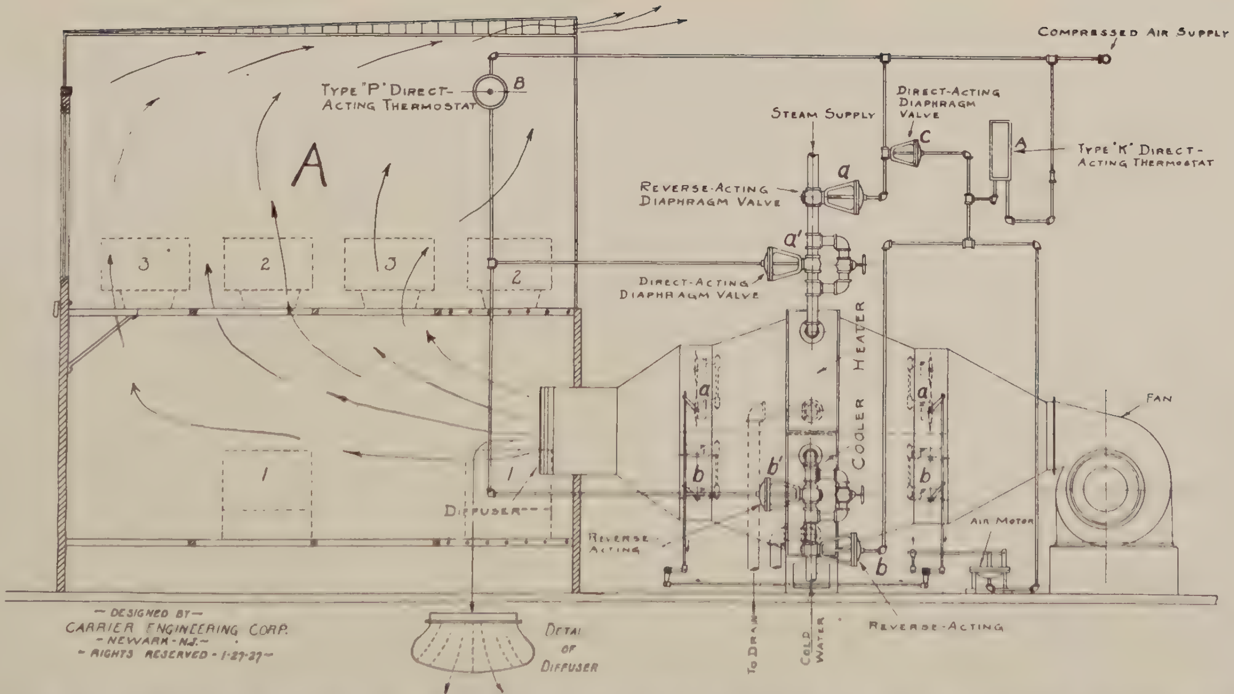


FIG. 166. A permanent Carrier designed unit. The one here described is planned to maintain 36°C. in room *A*. Thermostat *A* is designed to open steam valve, *a*, and damper, *a*, when the greenhouse temperature drops below 35°C. and at the same time close cold water valve, *b*, and damper *b*. The reverse of this is to occur when the temperature of the greenhouse exceeds 35°. The same principle is to be used with all other units down to 20°C.

Thermostat *B* is designed to control valves, *a'* and *b'*, that is to control the quantity of steam or cold water admitted to the heating or cooling coils, according to demand.

The type *K* thermostat indicated on the drawing as *A* is designed either to open completely or completely close the valves and air motors connected to it with a variation of 1° or 2° in temperature. In other words, it is not designed for graduated action since graduated action would be undesirable in this instance.

Diaphragm valves *a* and *b* are both reverse acting. In order to permit this an additional direct acting valve is interposed, indicated on the drawing as *C*. The reason for having both of these reverse acting is to provide complete closing of all steam and brine supply lines should the air supply pressure to the type *K* thermostat be accidentally disconnected. This, of course, is to prevent over-cooling or over-heating of animals in the small house. It would

about 75 cubic decimeters capacity, or 50 by 50 by 30 cm. For each of these cages a special humidity control should be provided. As explained in Chapter X, humidity should be controlled by saturating air at certain temperatures and then warming it to the proper temperature to give the desired humidity. This may be accomplished by causing the air which enters the chamber to atomize the water used in saturating the air (fig. 168). The writer has

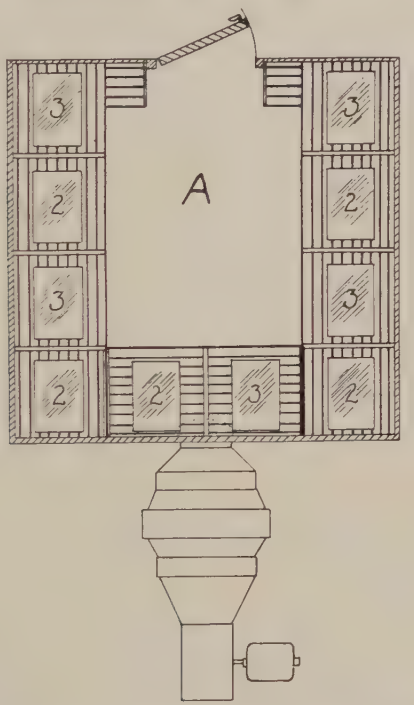


FIG. 167. Detail of room *A* showing cages placed on shelf and heater and cooler fan in rear.

conducted a series of experiments designed to test this idea. A glass-sided chamber, 30 by 30 by 50 cm., was placed above a box, 15 by 30 by 50 cm., completely filled with water. Air was introduced into the chamber at one end through a tube 4.5 mm. in diameter, which passed over three small capillary tubes just above the surface of the water. Allowing 1280 cc. of air to enter per second gave a velocity of 80 cm. per second past the capillary tubes and atomized

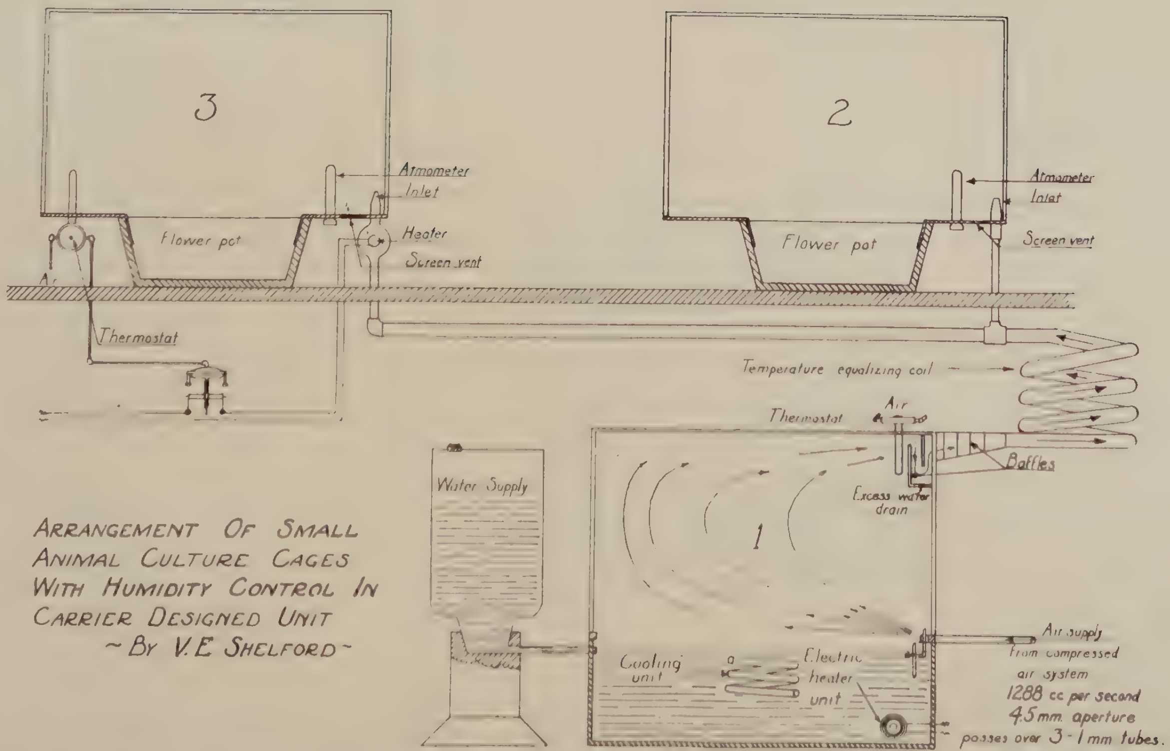


FIG. 168. Detail of two cages with humidifier unit attached. Each set of two cages has an air conditioner as shown. Five such units go in a room such as *A* in figure 167.

the water satisfactorily, so that the air in the glass chamber was saturated. The slot through which the air was allowed to drift out, showed a sufficient effect upon the transmitted light to make the difference clearly visible to the eye. There is no doubt that this method of atomizing water can be installed successfully. With the water held at a constant level and a constant temperature by means of electric current or circulating brine, any necessary dew point may be obtained by means of a thermostat. The difficulty encountered lay in controlling the flow of air through the experimental cage at the above rate. Air movement through the cage was calculated on the assumption that by the time the air reached the center it would be moving at a uniform rate lengthwise, but in the lower half of the cage its cross-section gave a very small rate of flow. On the other hand, an anemometer placed in the same position in which a plant would be growing showed a high rate, much higher than is ordinarily desired. Thus for example, if 15 meters per minute is the approximate rate of air flow through a field of wheat, it would be desirable to duplicate this rate across a wheat plant on which experimental animals were feeding. To accomplish this, some special method would have to be devised such as the use of small carrier ejectors pointing upward or a part of the air treated would have to be wasted or have to be used in other experiments, as indicated in the plan (fig. 168).

The use of air treated to provide a particular humidity at two different temperatures in two experimental cages desired to be held at several different humidities, is possible with a small addition of moisture. This is evident from the study of temperatures and humidities at which experiments must be run as shown in figure 126, page 276, which are based on outdoor warmings accompanied by evaporation from plants, the soil, and water surfaces. Under experimental conditions it is necessary to warm the air and at the same time add a small amount of water vapor from an open dish or wick with manual adjustable exposure. Thus air treated for 60 per cent humidity at 20°C. can be used for 25°C. and 47 per cent by the addition of enough moisture to raise the relative humidity 1 per cent. This is ordinarily added from the soil. (The heating of such air to 25°C. gives 46 per cent humidity and the average for such a rise in the growing season for southern Illinois is 47 per cent.)

The units shown in figure 167 are represented as long and narrow,

but cubical units may be used, or they may be made full shelf width and twice as long as shown, if the second temperature is omitted. Such units could be used for rabbits or poultry, with the same system of control.

b. Units for larger animals. Wherever experimentation on animals as large as cattle is desirable, there is every reason to make the facilities such as are shown in figure 162 which are 3 by 6 meters so that cattle may be accommodated as well as smaller animals, at least down to limits of those that may be confined by poultry netting. This necessitates adequate drainage and means of flushing the floor as well as ventilation and temperature and humidity control. For these rooms the ordinary methods used in conditioning rooms may be employed and installed by the Carrier Corporation. For such units, *a* to *j* of figure 162A, are proposed for five temperatures and two humidites for each temperature.

V. PROVISION FOR OUTDOOR EXPERIMENTATION

Every climate simulation laboratory should be provided with an outdoor field and garden space and particularly with such space adjacent to an air-treating plant (preferably subterranean) which can make possible the discharge of warm or cold air, or moist or dry air, at a constant rate over particular areas. The spraying of fixed amounts of water takes the place of rain. Of course, it is obvious that such experiments can be carried on only with relatively large animals for which screen of coarse mesh can be used to prevent their escape, or with very sedentary species. Nevertheless, the method would be a very valuable one. One very important essential for certain kinds of experimental work on small mammals would be a cage with roof and sides of quartz, so that all radiant energy could be brought to bear upon a given set of animals at a somewhat higher temperature than the surrounding air. Such a cage of fused quartz plate, however, would cost several hundred dollars even though it be of small size.

If ray filters are to be used, the special glass may be put in the sides of the small units, thus reducing the expense of purchasing and setting small panes of glass, in large rooms. The intensity of radiant energy, however, will be reduced by the two coverings of ultraviolet-transmitting glass.

The garden space should be extensive enough to supply *natural*

habitat for the various animals kept under experimentation; for, no matter how elaborate the experimental conditions may be, the final control is nature's out-of-door laboratory. One of the outstanding objects of investigations of this sort is to determine what factor causes the fluctuation in the abundance and virility of animals in the state of nature. The more natural territory on which such fluctuations may be observed, the greater will be the value of the results.

VI. THE LABORATORY

There should be a well-built laboratory in connection with the climate simulation plant. Much biological work on animals not requiring sunlight may be carried on in such a building. There may be constant-temperature chambers, incubators, etc. These hardly require description, as they are easily installed and constitute the small equipment of all well-equipped laboratories.

Laboratory space is necessary for the following purposes:

(1) For housing the recorders connected with the continuous measurement of the various physical factors.

(2) For checking the calibration of physical instruments. (a) A laboratory to house the various standard lights and instruments for measuring light (see p. 363). (b) A photometry room. (c) A dark room and laboratory for photography. (d) A flat roof with a small house built upon it with a hemispherical roof and quarter-sphere opening for standardizing instruments in sunlight (fig. 162A). (e) Chemical laboratory for the analysis of soil, air, and water. (f) Chemical laboratory for the analysis of the foods and of the plants and animals grown. (g) A bacteriological room. (h) A room for physiological work on birds and mammals. (i) Museum room for the storage of the animals collected, bred, etc. (see p. 56).

VII. EQUIPMENT USED AND ITS DEFECTS AND THEIR REMEDIES

The plans described on the preceding pages are correct in principle, as shown by the experience of the most successful engineers working in the field. The methods, so far as possible, have been modified to adjust them to the small units necessary in confining small animals and in running the large series of experiments necessary in work on insects and other animals to make the results of value to agriculture. The apparatus with which the writer has worked was not constructed in the main according to correct principles, and much of it can not be

recommended. However, investigators must assemble equipment from available materials and from parts abandoned for other purposes, basing their work on incorrect principles in many cases, because they lack funds to provide the needed facilities. Therefore, with a view to presenting as many principles as possible, and in some cases obviously for the purpose of pointing out failures and defects, the apparatus used by the writer will be described. Attention will be focused, first, on a system used at the University of Illinois, its imperfections and the difficulties encountered; and, secondly, on a modification of this system, in which many of the difficulties are remedied on the basis of the experience with the Illinois units, with other equipment, and on the basis of experimentation.

1. The University of Illinois equipment

The Vivarium buildings at the University were planned and located in 1914, as one of the early projects of the kind. The ground plan is shown in figure 165. The general plan of the glass houses was based on the State entomologist's insectary, built in 1905, a small, square, two-story building facing south, bearing a greenhouse extension to the east and to the west, a plan quite unsuited to continuous lighting and modern work in general. In the Vivarium the situation is aggravated by the large size of the south unit and the winter shadows over the north unit. There is nothing wrong with south facing if the distance between the buildings is great enough (fig. 165). In fact, the buildings could be 200 feet apart if they face the south, provided the north laboratory is the one to be without shadows. The central brick house, however, makes the end glass-roofed portion *useless* for work in which all-day sunlight is required. The central building always casts a shadow onto the west glass house in the morning and onto the east glass house in the afternoon. The north glass houses are in shadow most of the day in mid-winter.

A revised plan with light house is shown in figure 165. The situation shown in this figure is an ordinary one met in almost any city. The grounds are half a city block, bounded on three sides by streets and on the other side by a wide alley. A large building across the alley on the north complicates matters because of its June early morning shadow. The main building is located in the foreground and consists of a brick structure about 100 feet long with two 40-foot greenhouses, one on each end. The building is 43 feet high. About

20 feet north of this building is a 24-foot house, 20 feet high, with a 20-foot greenhouse on each end and a 20-foot wire cage house at the end of each greenhouse. The main building and this small building are connected by an arcade. 30 feet north of the small building is to be located a 24 feet by 24 feet greenhouse reached by an arcade from the other buildings. This house is in the shadow of the rest of the group unless it is raised about 10 feet above the ground. If the floor level is 7 feet from the ground and the glass wall starts at table height or 3 feet from the floor a good house may be built which will be fully in sunlight on all possible days.

To determine the position of this 24 feet by 24 feet house it was necessary to sketch in the territory shaded at extreme conditions, viz., December 21. Astronomical tables give the azimuth, and elevation (90° minus zenith distance), of the sun for any latitude at any time of day, month and year. From these tables were determined the extent and direction of shadow cast by the sun at 12:00 noon and hourly periods before and after noon. By laying out these angles on a plan it was found that this building could be located as shown. A different situation occurs with the building on the north side of the alley for its worst shadow would be cast on June 21st when the sun was farthest north. Its shadow will not interfere with this 24 feet by 24 feet structure after 6:00 A.M.

2. Construction of greenhouses

The greenhouse used by the writer was the northeast house with center (roof) and side ventilators, and a door at each end. To facilitate air circulation, three fans were placed on the bottom of the side ventilator on the south. The room was provided with steam heat under thermostatic control (Johnson system).

The air in the room was not conditioned, and the temperature rose often to 43°C. and occasionally to 45° or even 48°C. in summer. The building to the south and the arcade to the southwest shut off the prevailing winds in summer, and this tended to render the temperature conditions more severe. The control of the ventilators was manual, but should have been thermostatic. The room should have been conditioned and held at outside temperature as a matter of economy in the use of water, and of refrigeration.

3. The roof

The roof was of ordinary glass sloping symmetrically from a peak at the center. The peak ventilators were hinged near the center and could be swung to a horizontal position. While very effective, they could not be raised to full opening without rain beating in from unexpected showers. One of the most objectionable features was the wide opaque area at the peak, which in June cast a shadow over some of the fixed units for a considerable part of the day.

4. Compressed air

The compressed air used was pumped with a large piston compressor at the University power house, three blocks from the Vivarium. It appeared to be satisfactory air, although doubtless for very refined work a better supply should be sought. It contained nothing which could be injurious, except a rather large amount of carbon dioxide in some samples. Only occasionally there was a slight odor from the oil used in the pump, which was partly decomposed under pressure. This odor was not present when the best grade of oil was used, nor when a large amount of air was withdrawn. This air for nearly all of the work was reduced to 3 to 5 pounds, from between 60 and 80, the reduction being accomplished by the Mason valves for reducing pressures to below 5 pounds. These valves have an advantage over other valves that have come to our attention, as they give practically constant pressure regardless of fluctuations in the initial pressure and in the rate of flow through the valve.

Refrigeration was accomplished by Audiffren sulfur dioxide machines (a French patent) described in Chapter VIII. Their record for long efficient service is difficult to duplicate. The machines used were of 2-ton capacity, the largest made. Two of these were in operation. The refrigerating machines, being under thermostatic control, automatically stopped when the brine temperature fell to about $-8°C.$, and started again at a rise of two or three degrees.

The brine was circulated by reciprocating pumps that ran continuously. These pumps were probably responsible for much of the difficulty with the brine system, due to sucking in air. Centrifugal pumps should have been used.

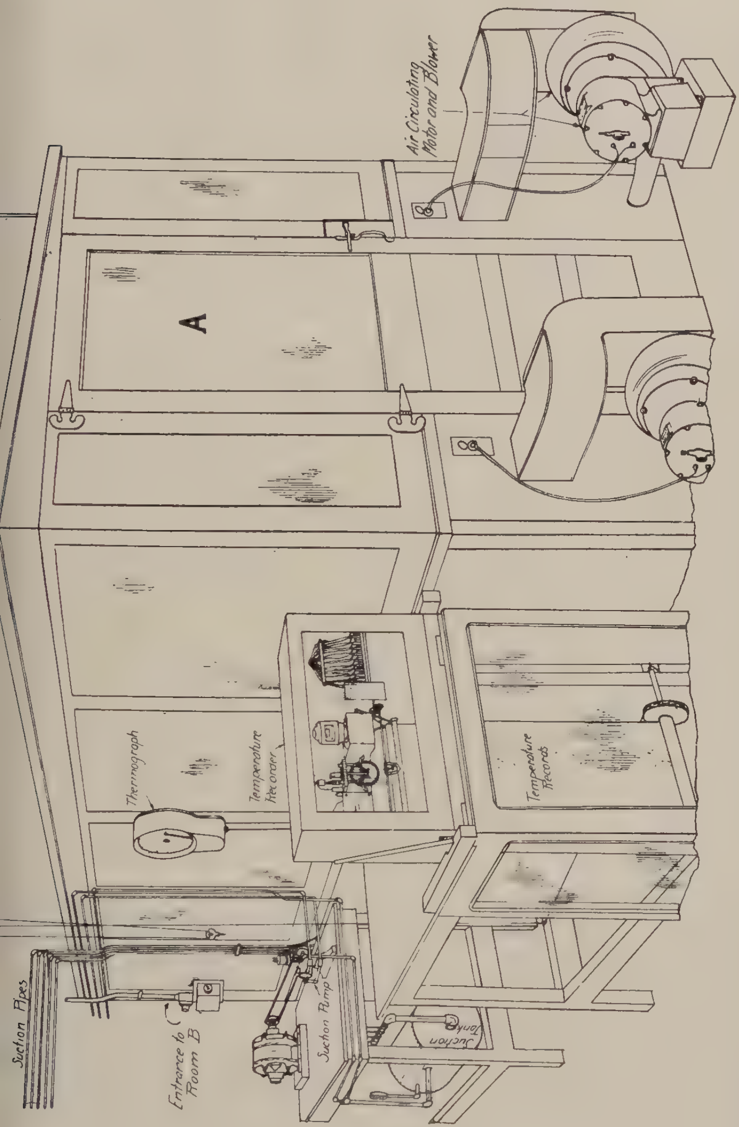


FIG. 169. Constant-condition chambers *A* and *B* as seen from the west end (University of Illinois, Vivarium). The blower fans draw air from the chamber through the square duct and force it through the round duct over the refrigeration coils, and to the top of the chamber. The motors are stopped and started by a thermostat. The temperature recorder records the temperature in ten different experiments. The rotary suction pump is operated by a motor and maintains a partial vacuum in the suction tank. Prepared by Illinois State Natural History Survey.

5. Constant temperature units

Except for the duct work of the tinners and the carpenter work, the units were constructed from commercial equipment, which consisted chiefly of the valves and thermostats and humidostats of the

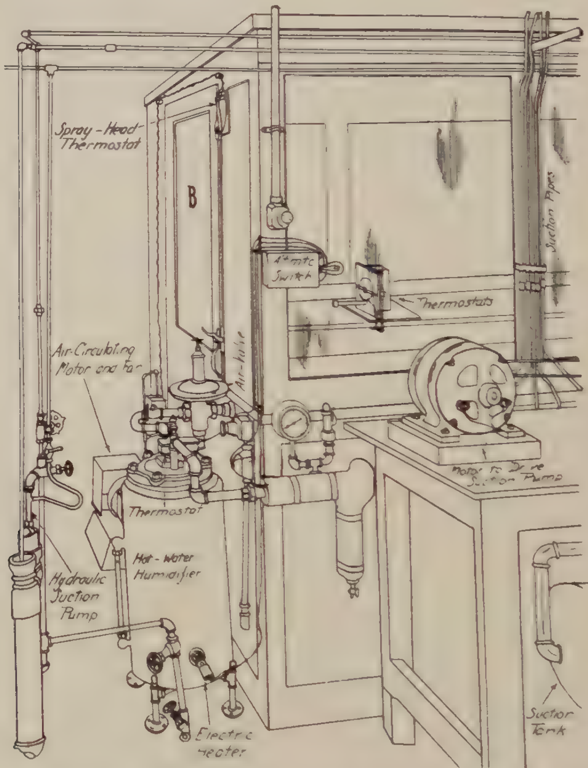


FIG. 170. East end of constant-condition chambers *A* and *B*, seen from the northeast. The equipment shown in figure 169 is in part repeated with full details of exterior of hot water humidifier (figure 171) and with hydraulic suction pump. Blower-operating thermostat shown through the glass. Prepared by Illinois State Natural History Survey.

Johnson Service Company, and the blowers of the Buffalo Forge Company. Figures 169, 170, 171, 172 show the plan and exterior of the units.

The chambers, figures 169 and 170, were of wood 4.5 by 1.5 by 2.1 meters (15 feet by 5 feet by 7 feet high) inside measurement

h doors at the ends. The unit was divided into two chambers, (A) 1.8 meters (6 feet) and the other (B) 2.7 meters (9 feet) g. The lower half of the wall was double and filled with sawdust l shavings. The upper half and top were of triple, double-ength window glass. (This should never be resorted to if avoid-e, on account of light reduction. If, however, it is found neces-y, the outer and inner glass must be removable, in order that all y be kept thoroughly clean.)

The interior of each chamber consisted of a long central aisle, h a 45 cm. shelf (S) on each side. The chamber was barely large ugh for two persons to enter and work at the same time.

The temperature was maintained by air recirculation over the ne coils (BC) by a motor-driven fan, and out through circulating ts (CD). The circulation units are shown in figure 93, Chapter I. There were two of these in the smaller unit, which was ended to run at 4.5°C. with the outside temperature at 40°C. ch coil was rated as having a refrigerating capacity of about 427 large calories (45,350 British thermal units) per hour, or a al of 22,854 large calories (90,700 British thermal units), for the aller section; for the larger section, 9,400 large calories (37,300 tish thermal units) per hour. These coils proved very inefficient ause their surface was small and because moisture blocked the s with ice (see p. 200). (It is more desirable to use cold water just ve the freezing point for the cooling medium.) The refrigeration s as calculated and installed were not adequate. Nearly as ch more refrigeration would be needed to maintain the tempera-e of 4.5°C. and 21°C. in the respective units. The difficulties in ne circulation discussed in Chapter VIII, page 203, were also ortant. The coils should be formed and carefully arranged so as prevent freezing shut, if brine prove necessary. The air should s at right angles to the pipes instead of parallel with them. ofin pipe affords a solution (fig. 75, p. 201).

The longer room was intended to be capable of running at 21°C. n the outside temperature at 43°C. The refrigeration was in-icient in summer when the sun was shining on the units. As plementary cooling devices, Shutte-Koerting 22 mm. atomizer y heads with $\frac{1}{4}$-inch pipe connection were installed. Each group ve spray heads was provided with a strainer which removed dirt n the water. The flow of water was under automatic control,

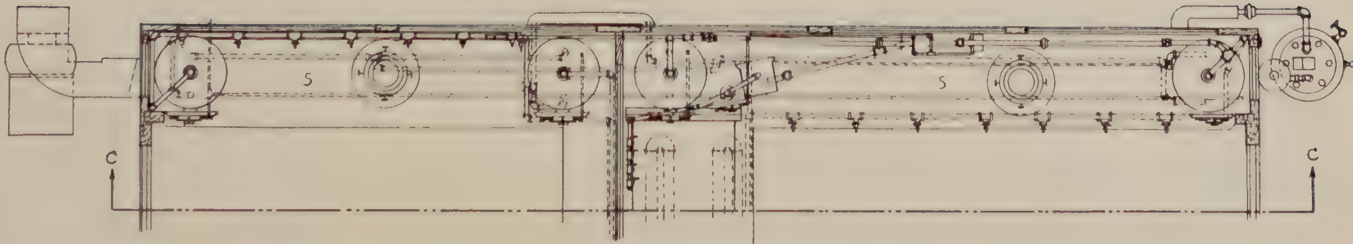
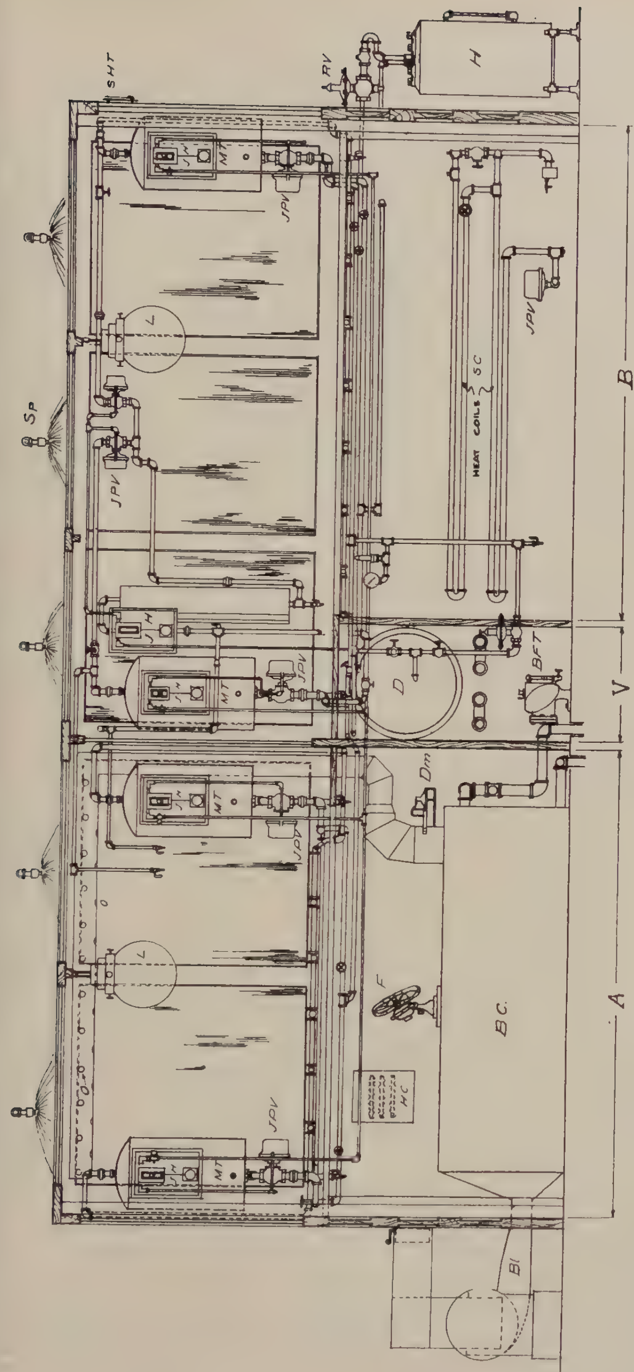


FIG. 171 *a*

FIG. 171. Showing climate simulating apparatus for constant conditions (University of Illinois, Vivarium). The north half is shown in the lower drawing as it would appear when seen from the south with the south half removed.

HC, heating coil; *SC*, steam coil; *BC*, brine coil to cool air; *JH*, Johnson humidostat; *MT* tanks to mix dry and moist air; *L*, artificial daylight globe light; *H*, hot water humidifier; *BFT*, trap to let water out of the de-humidifier; *Bl*, blower (motor and fan to circulate air); *O*, outlets for cooled air. Prepared by Illinois State Natural History Survey.



Section on "C-C"
FIG. 171 b

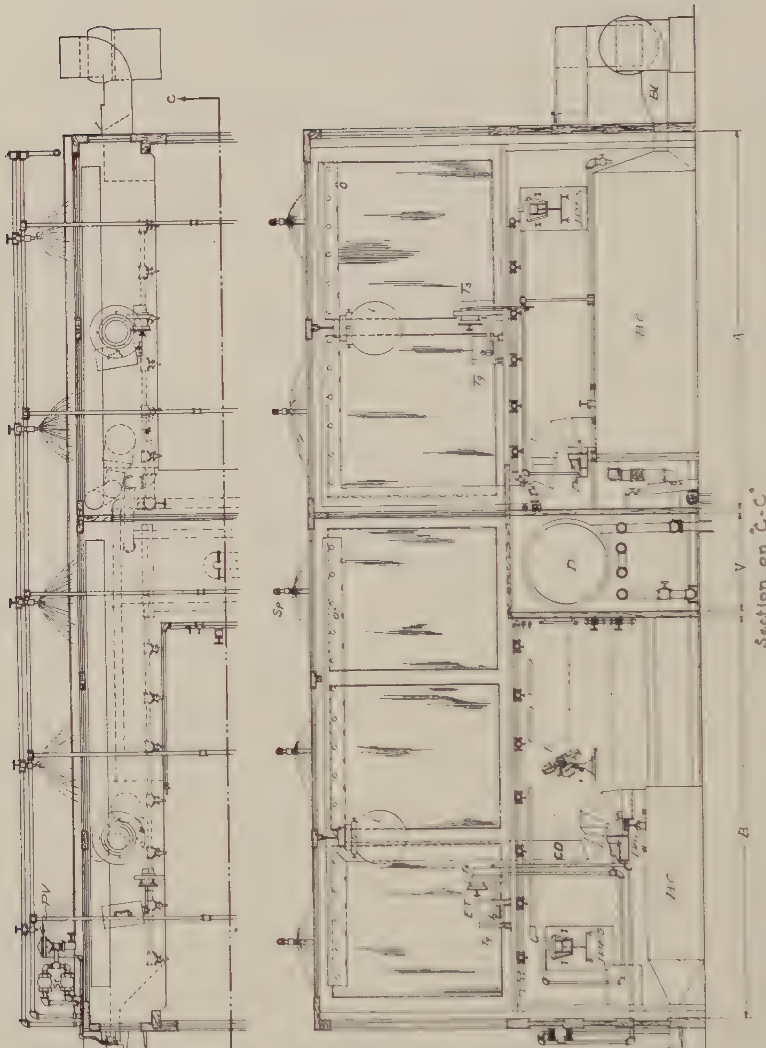


FIG. 172. Showing climate simulating apparatus (University of Illinois, Vivarium); units *A* and *B*, same as figure 171 but south half *TS*, thermostat for temperature in rooms; *JPES*, air switch for air circulating motors; *Bl*, air circulating motor and blower; *HC*, electric heater for room; *F*, fan to circulate air in chamber; *D*, dehumidifier horizontal; *Tg*, thermographs; *L*, artificial daylight globes; *O*, outlet

valves being closed and opened by a Johnson air valve, controlled by a three-point electric thermostat ("spray head thermostat" *SHT*, fig. 171) and a Johnson electric pneumatic valve (*EPV*, fig. 172), operated with batteries. The thermostat at times was placed inside the larger chamber, and at other times outside, and was so adjusted that the spray was turned on when the temperature rose above a certain point. This spraying system was merely to economize refrigeration and was not used at all times. It had the effect of reducing inside temperature by about 10°C., but it materially reduced the sunlight, especially because the well water used contained quantities of lime and iron, which covered the glass with deposits. The plan is one that should not be adopted where it can be possibly avoided. It proved a great nuisance, wasted water, and reduced light intensity. The light reduction made necessary the use of artificial lights (*L*) inside the units. The two 500-watt lamps produced 857 large calories (3400 British thermal units) per hour in each chamber, but the units could be run at 21°C. and 28°C., respectively. These lights were placed directly above the center of each shelf as shown in figures 171 and 172 (*L*). They were nitrogen-filled 500-watt Mazda lamps, covered with daylight glass globes which were recommended by the manufacturers (Nela Specialty Company) as being especially accurate in their production of daylight equivalent. The lamps, however, supplied light amounting to less than one tenth of sunlight and they were later abandoned for floodlight projectors (see p. 355).

The duct recirculating cooling systems were unsatisfactory. In cool weather in summer the temperature of the rooms fell at night to that of the surrounding greenhouse when some supplementary heat was not provided, indicating the inadequacy of such a system of regulation. Two heaters were provided in the larger, warmer room to maintain the night temperature. One of these was a steam coil (*SC*, fig. 171) operated by a Johnson thermostat and valve in the same way that an ordinary automatic radiator operates. This could be set so that the heat would come on when the temperature of the room had fallen about one degree below the temperature at which the blowers were set, and at the same time the steam and refrigeration would not both be in operation together. It seemed to be necessary in connection with the steam coil operation to install a three ampere Chicago Surgical and Electrical Company heater

with a thermostat (*ET*, fig. 172), the condition being that this thermostat would turn on the heat coil with a drop of a half degree below the temperature at which the refrigeration thermostat was set. The colder room also had an electric heater (*HC*, fig. 171) with thermostatic control. The use of two thermostats is undesirable; it gave irregular temperatures and was a nuisance generally. The second thermostat should operate outside.

To provide a third temperature a small heater covered with very fine screen was placed in one of the glass cages but this was not regarded as a success. The introduction of small refrigeration coils into certain cages would have been practicable, but these were never used.

These rooms were supplied with compressed air. The compressed air entered the chambers under high pressure (60 to 85 pounds) and was divided into two lines. One of the lines led through a dehumidifier (*D*, figs. 171, 172) shown in Chapter X, figure 111. Dehumidification was accomplished by brine circulating through a coil about which the air was passed. This gave much trouble because of ice frozen on the pipes.

To supply wet air, another line of high pressure air passed through the chamber, the pressure was reduced by a Mason regulating pressure-reducing valve (*RV*, fig. 171). After reduction, it passed through a tank hot water humidifier *H*, (see figure 171 and figure 170) containing an immersion water tank heater under thermostatic control. The control consisted of a Johnson insertion electric thermostat with a William H. Smith relay switch. This heating apparatus was sometimes not operated during the summer months, when a large amount of air was used. Both wet and dry air lines were supplied with pressure gages and pop valves set a little above the pressure in use to prevent the turning of a too high pressure into the equipment.

The air used in ventilating experimental cages consisted of a mixture of the wet and dry air. The mixing was accomplished in a galvanized iron tank 30 by 60 centimeters (*MT*, fig. 171), of a type commonly used as expansion tanks in domestic hot water heating systems. Into each tank a Johnson humidostat (*JH*, fig. 171) was inserted. The humidostat operated a direct and reverse Johnson pneumatic valve. These were so arranged that when the air was too dry the pressure of the Johnson air supply was turned on to the

valves. This pressure opened the moist air valve, and at the same time closed the dry air valve. When the air was too moist, the opening of the leak port of the humidostat and the resulting humidostatic operation closed the moist air valve and opened the dry air valve. There were five mixing tanks in the two chambers, one for dry air and one for wet air in each chamber, and in addition a smaller tank with humidostatic control which mixed the air from the two tanks in the larger chamber and produced an intermediate humidity. The dry air from the colder chamber was carried through the wall of the warmer chamber, where the rise in temperature gave it a still lower humidity. The dry and intermediate air of the warmer chamber was conducted into the colder chamber, where under the same conditions a humidity intermediate between the extreme wet and extreme dry air was afforded. The transfer of air from one temperature to another to give more humidities is an important principle. With the humidostats operated at their best, the humidity as shown by the records of the hygrographs varied from 2 to 4 per cent, between the turning on of the wet, and turning off of the dry air, and vice versa. More often 10 per cent difference occurred. In general, this method of controlling humidity can not be recommended.

One difficulty with the humidity system was experienced in keeping the wet and dry air pressures the same. When set so that ordinary gages read the same there was still considerable difference in pressure of the air used in the mixing tanks. This made difficulty at times, and on a few occasions caused peculiar cross leaks. The humidity was not satisfactory due to the great difference in the two humidities mixed in the humidostatic tanks. There should have been several humidities to mix with steps of 10 per cent to 15 per cent instead of two with 60 per cent difference. The direct closing and opening of the Johnson valves is undesirable even with the small steps. Originally humidostats were not designed to work under pressure. The Johnson Service Company designed an insertion humidostat to work under pressure (fig. 112, *A*, *B*, *C*, Chapter X, p. 255) and this together with the intermediate pneumatic control and valve gave constant humidities when the sensitive parts *were in the case with the recording instrument* and much better results than were obtained otherwise when the sensitive part was in the *mixing tank.*

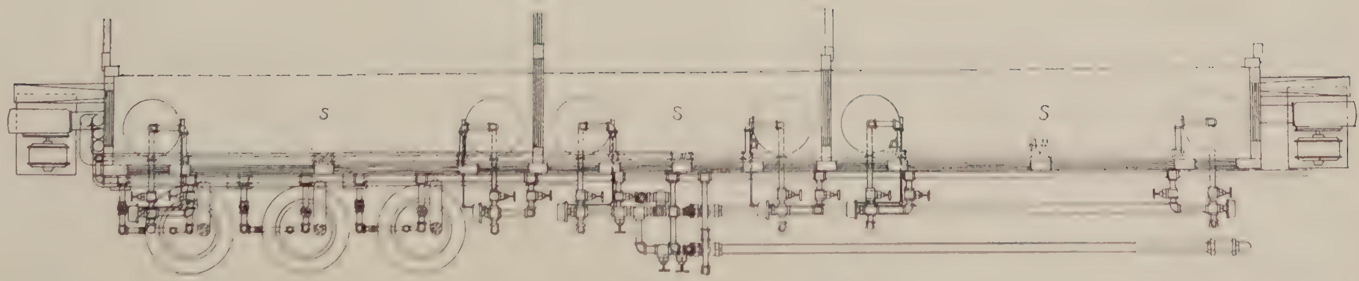
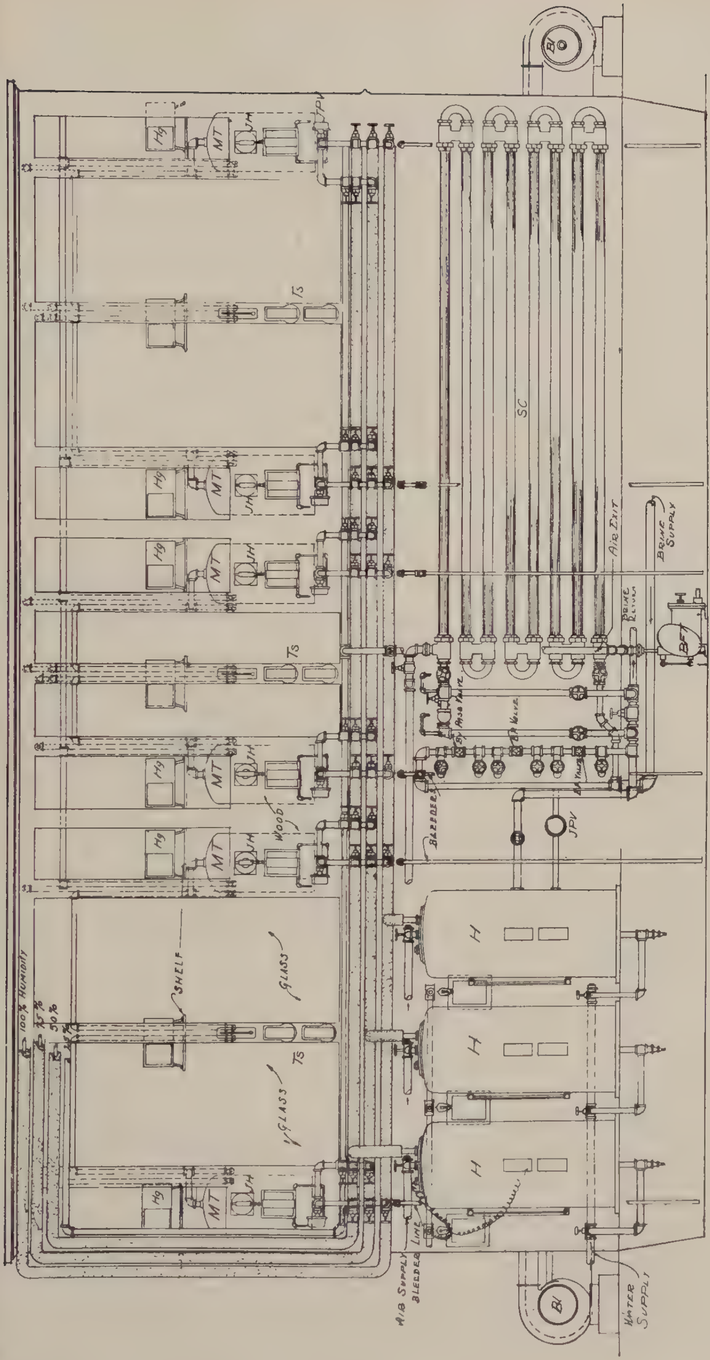


FIG. 173 *a*

FIG. 173. Showing a redesign of the Illinois equipment. Three humidifiers are provided, two with heat and one with refrigeration. The double pipe coil is for producing very low humidities, and is provided with a ball float trap to discharge moisture. The mixing tanks, *M. T.*, for air of two humidities with intermediate humidostat (*JH*) and three way-valves (*J. P. V.*) connected to the air lines. All valve working parts project outside the unit. Small shelves are designed to hold hygrographs over the hairs of which a leak from the mixing tanks indicates the humidity at all times. For meaning of other letters see text and figs. 171–172.



100% HUMIDITY
75%
50%
Hg
MT
JH
TS
SHELF
GLASS
WOOD
BLEEDERS
JPV
SC
AIR EXIT
BRINE SUPPLY
BRINE RETURN
BFT
H
BI
AIR SUPPLY LINE
BLEEDER
WATER SUPPLY

FIG. 173 b

6. *Improved design for constant-temperature units*

A new set of units was designed on the basis of the experience with the old ones and some of the improvements installed (figs. 173 and 174). The general plan calls for increasing the height of the unit so as to make the roof an integral part of the roof of the green house with only one thickness of glass above. It is divided into three units *A*, *B*, and *C*, for three temperatures. The center and coldest room, *C*, is to be entered from the room intermediate in temperature, *A*, figure 173. The interior shelves are as in the other units. The duct cooling devices with cold water pipes of finned cooling coils are set in "stagger" arrangement (fig. 173). The floor is raised and free along the sides making a cold chamber in the center from which the air is drawn by the blowers. The ducts (fig. 93, Chapter VIII, p. 220) leading upward from coils are omitted in the drawings. The brine coils are arranged in series so that when there is circulation through one there is circulation through all. Coils can be cut out by opening by-pass valves, in figure 173, and closing the valves to a pair of coils.

The air supply is designed to be from a Nash hytor with pressure at about 3 pounds. Three humidifiers of the type shown in figure 112, Chapter X, are provided for. One to be run at 30°C., another at 20°C., another at 10°C. The two are provided with heat coils and one with a small cold water (2°C.) coil, all under thermostatic control.

The dehumidifying apparatus consists of a double pipe cooler such as is commonly with ammonia refrigeration machines. Cold water or brine circulates around the central pipe through which the air passes. This unit is in duplicate to make possible thawing the ice from the pipes when brine is used. The moisture is discharged into a ball float trap shown below the coil.

The mixing tanks under humidostatic control and the piping are arranged so that air from any of the dehumidifiers or humidifiers can be introduced into them. They are controlled by intermediate humidostats in the mixing tanks and three-way mixing valves.

The dials and control portions of all equipment are brought to the north side of the unit, and a thermometer showing the temperature in the units has its scale outside. To keep a constant check on the humidity, hygrographs with the sensitive hairs enclosed in a small flow of air from the tanks are provided for and placed in full view from the north side of the unit. Most of the improvements suggested in

this design have been tried out in the suggested form or some other form and give promise of remedying the more serious difficulties with the old units. By passing the air of a particular humidity of each

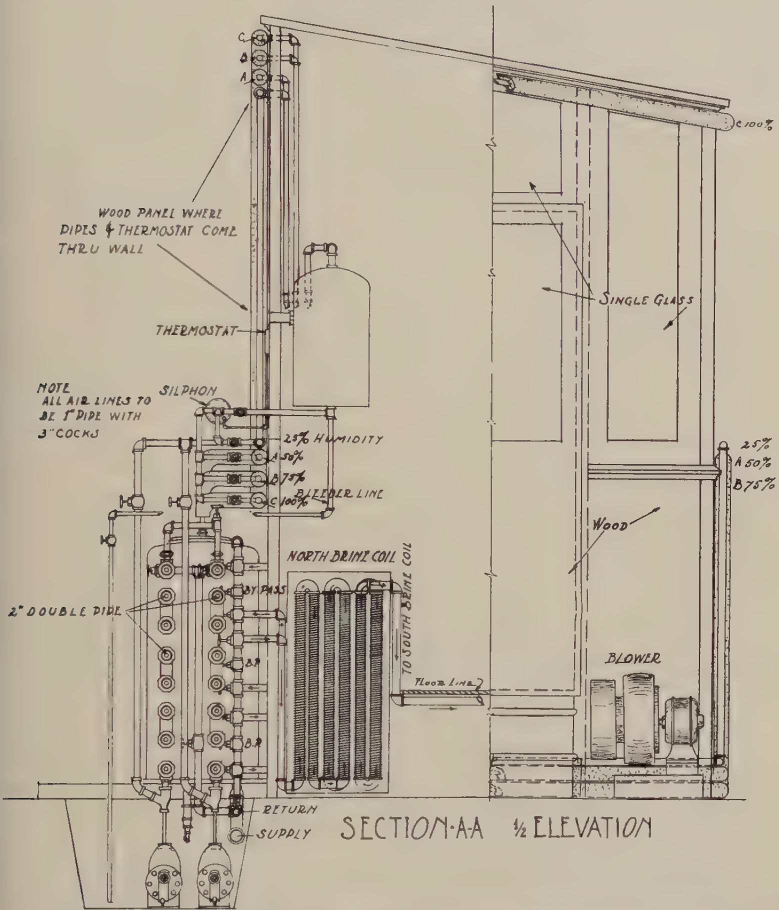


FIG. 174. Showing the end view of the same apparatus shown in figure 173. End is cut away showing the brine coil, duplicate double-pipe dehumidifier, etc.

room from each tank to the other two rooms from four to six humidities can be secured for each three temperatures. Single thickness glass is designed to remedy the defects indicated in figure 175.

The air supply for such a unit is shown in a diagrammatic assembly (fig. 176), when the system actually used in the units shown in

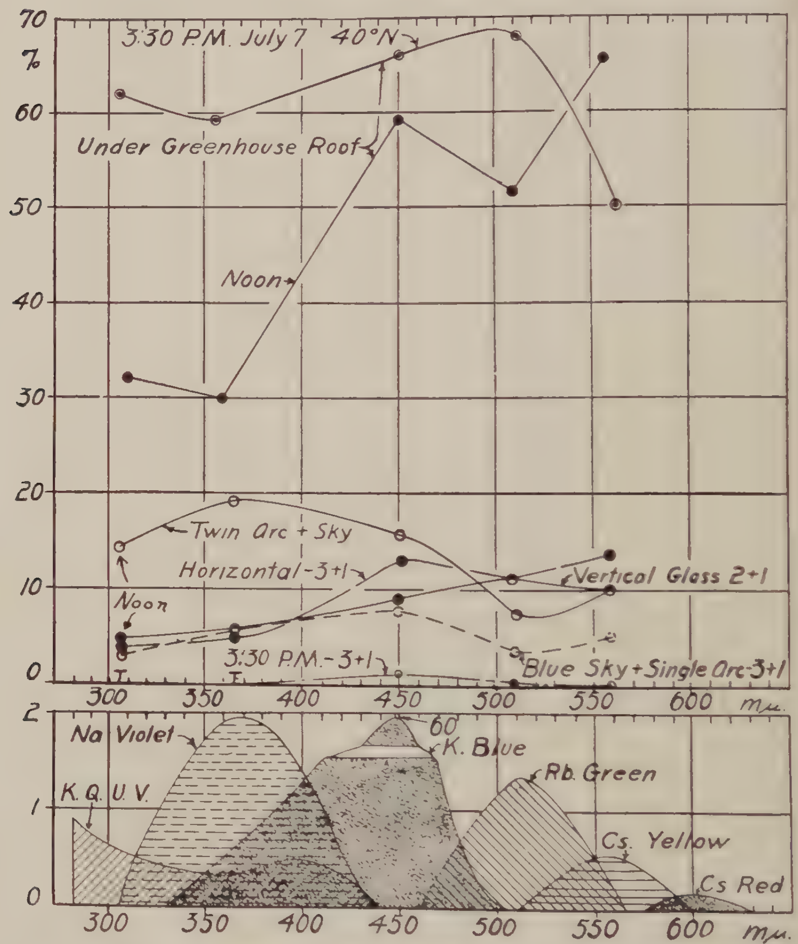


FIG. 175. Showing the effect of the glass roof and cage tops and sides on light intensity. The value of white flaming arc lamps is also indicated. Polygons below indicate the sensitivity of the photo electric cells to wave lengths. The roof appears to absorb more violet and ultra-violet at noon than in mid afternoon. The twin white flaming arc burning at 45 amperes gives more light than shown by the sun after passing through two vertical thicknesses of window glass plus the one thickness cage roof. Three plus one equals the three thicknesses of window glass in the top of the unit shown in figures 169–172 and cage roof.

figures 171 and 172 is adapted to the reduced pressure supplied by the Nash hytor. The water supply in the humidifying tank is renewed from a supplementary tank designed to maintain a constant level in the humidifier. The mixing tank is shown connected to both ends of the supply line. The connections to the mixing tank should be double, the pipes of large size, and the nozzles especially large. A $\frac{3}{4}$-inch pipe and $\frac{3}{8}$-inch gate valves are desirable. Figure A shows the design of a piston leak to equalize the pressure in either the various humidifiers or mixing tanks. With the exception of the dehumidifier, the apparatus cannot be recommended.

VIII. VARIABLE-TEMPERATURE EQUIPMENT

1. Desirable Apparatus

This should be constructed exactly as the constant temperature units designed by the Carrier Corporation except that a program thermostat should be substituted for the type *P* thermostat in figure 165. Care should be exercised to see that the units can vary 30°C. between day and night. In summer, there is little difficulty in securing sufficient daily range in temperature, etc., in an *unconditioned* greenhouse and the section used for variable-temperature experiments can probably be run more economically if not conditioned during the period of such experiments, though it should be possible to condition it when required. The use of the other equipment about to be described can not be recommended. Nevertheless, experience in constructing and running such experiments with such equipment has been valuable.

2. Provisional apparatus (663)

This apparatus originally used consisted of five chambers of a type shown in figure 177, but smaller and admitting only one cage. They were not constructed so as to admit the observer as the changes in temperature caused by opening the chambers were not regarded as serious at the time they were constructed. Three small chambers, which were 63 cm. long by 50 cm. wide by 105 cm. high, were designed first, and later found to be too small and were supplemented by larger ones, which were 100 cm. by 50 cm. by 120 cm. high. These small chambers were of two kinds, two with glass sides and one with opaque sides. Each consisted of the main chamber with a water

tank above, the water tank being provided with a glass bottom and glass sides so as to admit light through the water. The water flowed in through the water tank from the water supply and out through a waste pipe so as to maintain a water level a couple of inches below the top of the tank. This made it possible to supply cold running water to keep down the temperature of the main

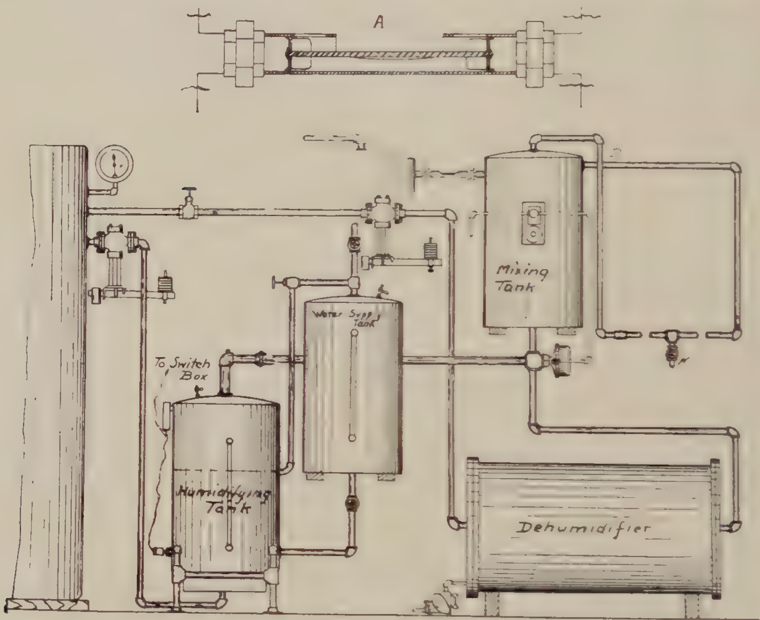


FIG. 176. A diagram of air supply tank, pressure reducing valves, dehumidifier, dehumidifier mixing tank, supply to cages connected with mixing tank at both ends with large pipe. A, pressure equalizer. Piston moves back and forth from high pressure side to low pressure side and pipe is slotted to allow pressure to leak off when the piston uncovers the slot. This automatically adjusts pressure in both tanks to same gauge.

chamber on hot sunny summer days. The main chamber was provided with a wooden shelf as shown in figure 177, leaving an opening from below the shelf up into the main body of the chamber when the door was closed. Under the shelf were coils which provided heat during the night, but ordinarily the sun caused the temperature to rise to about 37°C. on summer days. The chamber was supplied with humidified compressed air, introduced to ventilate the cages.

The wall of the chamber contained four small pipes ending in a slender hose-end on the inside and in a small 3 mm. cock on the outside. The purpose of this was to conduct the atmometer leads or suction leads through the wall. A similar dark chamber was provided. Difficulty was usually experienced in maintaining a temperature similar to that in the other chambers, which tended to rise higher during the day. The same mean temperature was obtained in this chamber as in the others, although it was done by

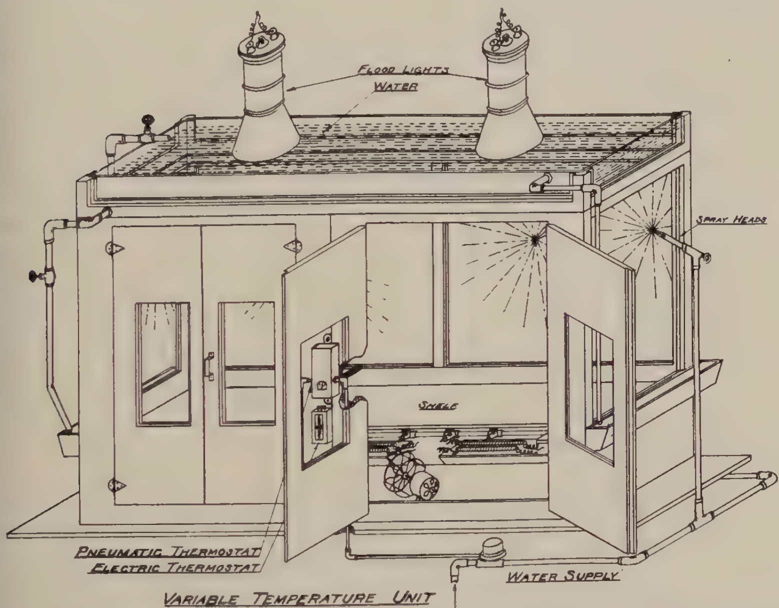


FIG. 177. Variable-temperature unit without refrigeration. With spray-head and water tank control thermostat (pneumatic) and electric thermostat for the heat, a circulating fan, and flood lights.

raising the minimum during the period of the night instead of by raising the maximum at midday.

The humidifying device which treated the air supplied to these chambers is shown in figure 110, Chapter X. It consisted of a galvanized iron cylinder so constructed as to stand pressure of from 5 to 10 pounds, into which the reduced pressure air entered at the right. In the top of this cylinder was a Schutte-Koerting spray head which sprayed cold water into the chamber through which the air passed.

This nearly saturated the air at the temperature of the water, which was about 16°C. during the summer months. The surplus water from the humidifying chamber flowed out through a ball float cock steam trap (Harding and Willard). The air passed over the galvanized iron cylinder through a moisture or condensation separator, which removed the water. This humidifying process supplied air nearly saturated at the temperature of the running water, and the humidity for any temperature above or below this could readily be calculated. This was experimentally ascertained for a period of several weeks in July, 1919, by allowing the air after leaving the humidifier to pass through a hood which was slipped over the sensitive parts of a Friez hygro-thermograph. The air was passed through a block tin pipe coil surrounding the temperature sensitive part, before passing into the hood entrance. This apparatus then recorded the temperature and the humidity which this air gave when raised to a given amount above the temperature of the water. These results seem to indicate that the air was generally above 90 per cent of saturation and that the calculations were approximately correct.

The separate units proved unsuccessful; it was impracticable to hold two of them at the same temperature. They could be combined in a single unit large enough to hold four cages of the size indicated below for growing plants. This makes possible the use of three cages for humidity experiments and one of them may be darkened so as to show light effects. (The dark chamber mentioned above was a failure; the temperature could not be maintained the same as in the light ones.) Cages exactly like the light ones but with the glass covered with blackened thin sheet copper are suggested as probably meeting this need. These units may be opened while records of the conditions of the animals are made without seriously disturbing the conditions. The entire constant temperature apparatus of the type used at the University of Illinois may be changed to variable by program thermostats.

At times one of the blowers of the cold room was disconnected and a thermostat switch inserted in one of the two wires, supplying it with current. The room thermostat was set at 20°C. and the extra thermostat adjusted so that when the temperature rose to 30°C., the second blower started to run and prevented its going any higher. When the temperature fell below 30°C., the blower fan stopped running. This gave a uniform night temperature with a tem-

perature climbing to 30°C. during the day and dropping back to 20°C. at night. Likewise the warmer room was sometimes run with variable temperatures; the spray head thermostat was so set that it turned the spray heads on when the temperature had climbed to about 34°C. which prevented it rising above 35°C. and gave a day with a uniform night temperature, and a rise to 35°C., at midday, dropping off again later in the afternoon. This was a temporary arrangement for giving easily described variable temperature days.

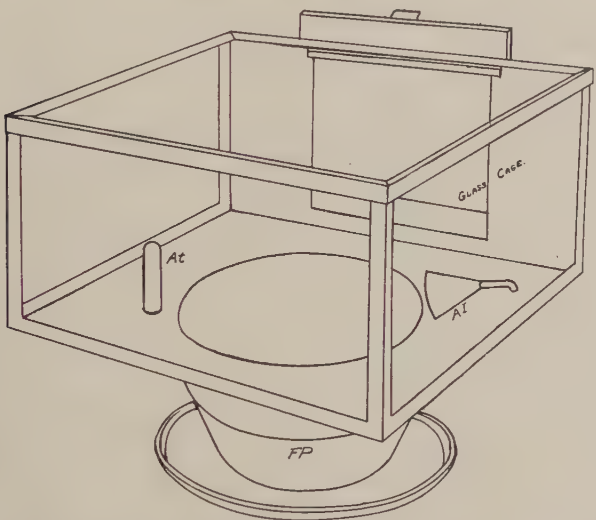


FIG. 178. Flower pot ventilated cage for small animals requiring food plants showing atmometer and air inlet. Such a cage should be at least 35 by 35 by 50 cm.

IX. CAGES AND CONTAINERS FOR SMALL ANIMALS

Granted means of conditioning air, regulating its flow and controlling the temperature, the next important consideration is the container in which the animals are to be held during the experiments. The character of these varies with the animal, or stage of the animal and its habits. Roughly there are four classes of needs for cages: (1) For animals not requiring light or food plants, such as insect pupae, insects feeding on dry grain, dead wood, etc. (2) For animals living in soil which must be kept in darkness, with soil moisture and aeration maintained and at the same time so located as to be visible to the observer from time to time. (3) For small mammals, reptiles,

etc., which require drinking water, quantities of solid food, and make necessary the removal of fecal matter. (4) For insects and other small animals requiring growing plants, etc.

Cages for growing plants are probably most commonly required. These cages are of glass sides and top and metal bottom, with a circular hole and flange to fit a large flower pot (fig. 178). A cage may be made by cutting the bottom from a battery jar. Air used to ventilate the cage is forced in through a narrow slit so as to distribute

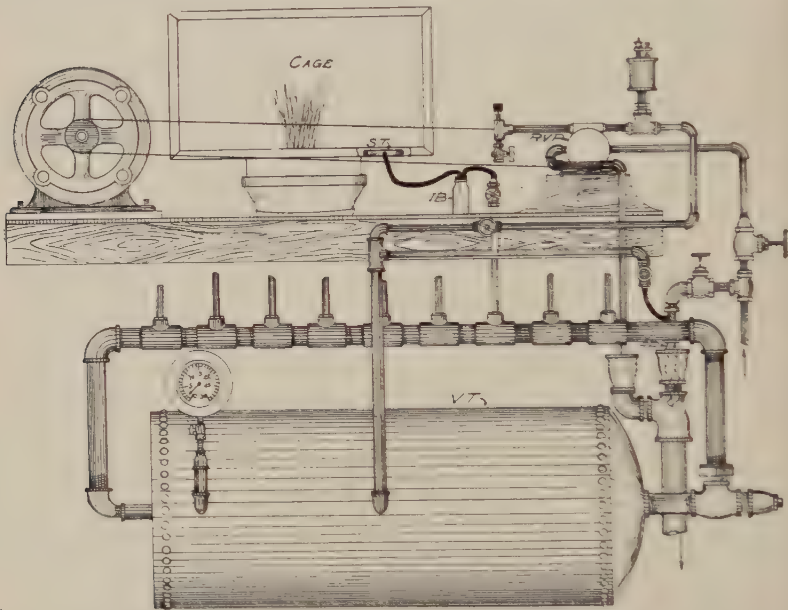


FIG. 179. Suction system showing method of connecting suction pipes. The unit is supplied with both rotary pump and water suction pump.

it. An atmometer is introduced from below. The cages should be large enough to take a Friez hygrograph. Cages 35 cm. wide, 35 cm. high, and 50 cm. long are adequate but nearly minimum in size for animals living on grasses. The size of the food plant has to be considered.

In such cages where general cultures feed on the plants in numbers, it is often necessary to isolate individuals. For this purpose a suction system, figure 179, was installed in connection with the chinch bug

work of the Illinois Natural History Survey, so that a number of cages could be supplied with suction tubes (ST). The tubes used were made from one arm of a U-chloride tube. A small screen was cemented over the hose end base and a cloth tied over the opposite end. The suction air was drawn through water so that the flow could be seen, it was checked and set at the rate of ventilation of the entire experiment (IB).

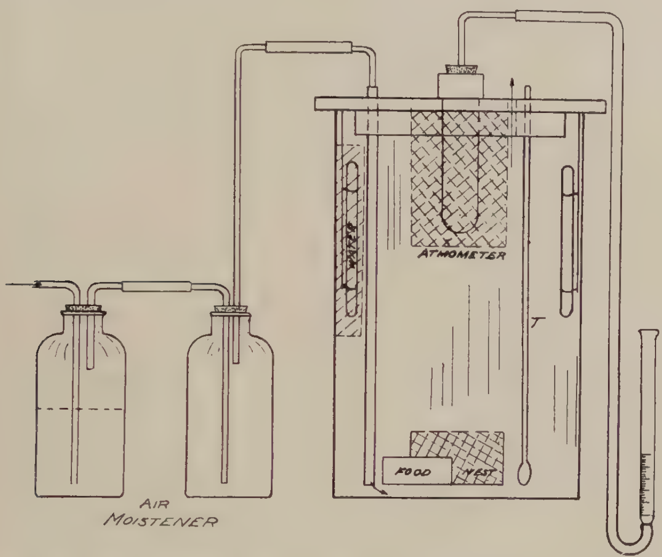


FIG. 180. Cage used by Dice (247) for experiment on wild mice

The second type, namely, that suitable for mammals has been little used. Dice (247) in his work on mice devised a method of keeping the animals in large battery jars equipped with water fountains, atmometers, nest, food box and thermometer as shown in figure 180.

X. PLANS AND FUNDS FOR PRACTICAL PROJECTS

Most of the research done the world over is the product of the spare hours of those who teach, lecture, answer inquiries in practical agriculture, write non-technical bulletins, etc. A much smaller amount is done by men employed primarily to do research and who do a little of the teaching. Relatively very little is done by men employed to devote all their time to the work. Many of these are in

government service and the opportunity and facilities for climatic and ecological work under government auspices appear to have suffered severely in the United States, at least since the Great War. There has been a tendency to devote government agencies to police work. It is obvious that climate simulation experiments can not be conducted on the scattered leisure hours of those primarily engaged in something else. The opportunities in endowed agencies are so limited that state and national resources are most likely to be used.

It is recognized that many lines of investigation must go on continuously. In addition, there must be intensive studies of certain species carried on. It is necessary to consider that the interest in such problems begins when economic losses are at their height and lasts only as long as the losses continue to be felt. Three years is about as long as one can expect interest, support, and enthusiasm for such a project. It is, therefore, necessary to plan to issue preliminary reports at the end of the first and second years followed by the final report a year later. If plans are not made and a staff is not employed so as to bring the work to a close at the end of such a period the results will not be good. Interest will lag: appropriations will be cut. Those directly responsible are likely to be left with a large burden of work. The resulting dissatisfaction on the part of those interested makes further study less likely to be supported. The only wise procedure where public funds are to be used is to make an estimate sufficiently large to cover the expense of about three years of work on an adequate scale. It is true that this has not been practicable in the past, as there was not enough experience to make such estimation possible.

We have already pointed out the necessity for extensive experi- mentation in uniform stocks. In order to avoid heterogeneity o results due to differences in stocks or different physiological con dition from year to year and from season to season and secure th best possible results, it is necessary to have adequate buildings grounds and equipment and a considerable staff of men. The write believes that the investigation of such a problem as the influence o weather and climate upon the European corn borer is well wort doing. With the idea of lending assistance to the control of th insect, it is worth doing on such a scale. To illustrate the needs an difficulties, let us assume that the investigation of the relations of th insect to weather and climate be undertaken. About $250,000 shou

be available if it were to be carried on in connection with an institution already partly equipped to undertake the work. Not less than $20,000 of this would go to build a suitable glass-roofed building adjacent to some ordinary laboratory where ordinary facilities would be available. An additional $120,000 would be required at the rate of $40,000 a year over a period of three years to pay the expense of the work and the salaries of three biologists and two engineers who would devote their entire attention to the problem. It would be necessary to plan to have the experiments repeated during three seasons in order to get sufficient weather variation to check the experimental results.

CHAPTER XVII

Physical Conditions in Water (Except Light)

I. INTRODUCTION (434)

The control of physical conditions in water is essential to successful experimentation. Hydrostatic pressure, movement in the form of waves and currents, temperature, osmotic pressure and light must receive their share of attention. The effects of pressures, movement of waves and currents, etc., upon organisms are important but have been studied little except with respect to behavior. Various animals make nests, etc., the character of which is determined by mechanical conditions such as currents. For example, the pupa of the black fly spins a tangled mass in the absence of current. Waves and currents may be duplicated under laboratory conditions. Some apparatus for the latter is described on page 80 in connection with a discussion of behavior.

II. VISCOSITY

The viscosity of water is of much importance in determining the ability of plankton organisms to float. Viscosity is used nine times in the denominator of Stokes' formula for the settling of particles. Temperature is the chief factor in the control of viscosity.

There are differences in the forms of plants and animals correlated with viscosity differences. Wesenburg-Lund (967) found differences in body surface, form, size of appendages, etc., in Bosmina, Daphnia and related forms, which he supposes to be due to seasonal differences in viscosity of the water. He shows figures of the form of such animals at different seasons. Gran has discussed this for marine plants, and Hjort, in the same volume (610) calls attention to the importance of viscosity of sea water to the ability of animals to sink or float.

1. Measurement of viscosity (267, 383, 384)

Viscosity may be measured with very simple apparatus. The Ostwald (639) tube shown in figure 182 and a modification with con-

venient cocks, known as the Drucker tube, are commonly used. Both involve the determination of the density of the liquid.

Viscosity may be measured conveniently, without density determinations, by a method devised by Scarpa (Farrow, 288) which obviates density determinations and permits the use of unequal volumes of liquid in the different experiments. As modified by Farrow, the method consists in measuring the time, t_1, which is occupied in drawing up, through a vertical capillary tube, sufficient liquid to fill a bulb at the top of this tube, and the time, t_2, which this volume

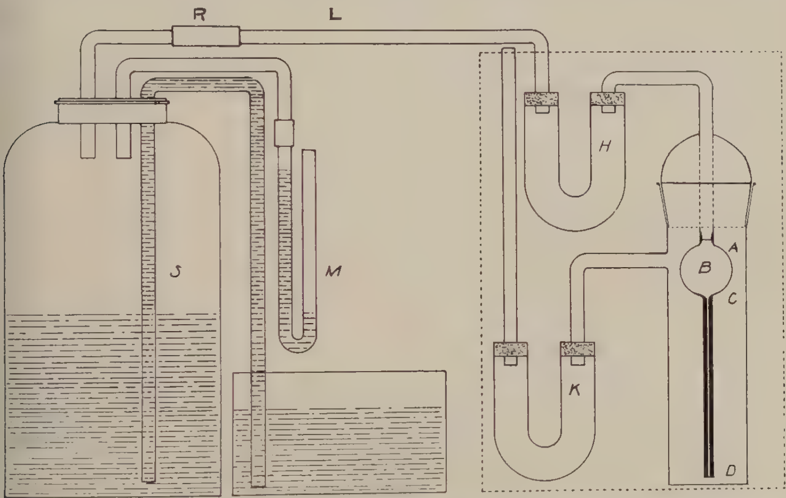


FIG. 181. Diagrammatic sketch (not to scale) of viscometer and accessory apparatus similar to that used by Scarpa (after Farrow, (288)).

takes in flowing out from the bulb under the weight of the liquid. Given constant conditions, the viscosity of any liquid is proportional to the expression:

$$\frac{t_1 \cdot t_2}{t_1 + t_2}$$

The form of viscometer used by Farrow was a modification of that used by Scarpa (loc. cit.). A ground-glass joint is substituted for the cork or rubber stopper of Scarpa's (777) apparatus. Figure 181 is a diagrammatic sketch (not to scale) of the viscometer and accessory apparatus. A is a glass vessel, with side-tubes as shown, and

with a glass tube sealed through its ground-in stopper. This tube is in connection with the bulb *B*, from the bottom of which leads the capillary tube, *CD*. *H* and *K* are guard-tubes containing loosely-packed glass-wool moistened with a dilute solution of sodium hydroxide. This packing serves to prevent access to the experimental solutions, of carbon dioxide, and of dust, and at the same time checks distillation from, and consequent concentration of, these solutions. *K* is open to the air on one side, and has a glass tube carried from it to a point above the water surface of the water bath, while *H* can be joined, as shown, to the aspirator, *S*. The connection (a rubber tube) between *R* and *L* can be removed at will, while *R* is closed by a spring pinchcock. Suction is applied to *L* in order to fill the viscometer bulb after the apparatus has been charged with experimental

TABLE 46

Dimensions of viscometers used by Farrow

VISCOMETER	VOLUME OF BULB	DIAMETER OF CAPILLARY	LENGTH OF CAPILLARY
	cc.	*mm.*	*cm.*
I	8.2	0.4	10.0
II	4.5	0.6	9.5

solution. The suction exerted depends on the difference in level between the water in *S* and that in the outside dish. The measurement of this suction is effected by the water manometer, *M*, which is made to give the same reading constantly. Final adjustment of the suction is effected by adding to, or withdrawing from, the water in the open dish.

The parts of the apparatus surrounded by a dotted line are enclosed in a water bath. The viscometer is clamped in a holder designed to secure its accurate vertical adjustment.

Farrow used two viscometers of this design, of which the essential dimensions were as shown in table 46. For all measurements the viscometer was sunk in a gas-heated water-bath with glass sides. The temperature of this was maintained at 70 ± 0.05°F.

The viscosity *n* is calculated in accordance with the formula:

$$\eta = \frac{\left(\dfrac{t_1\, t_2}{t_1 + t_2}\right)_s}{\left(\dfrac{t_1\, t_2}{t_1 + t_2}\right)_w} \cdot \eta_{w_1}$$

here s and w indicate solution and water, respectively.
Actually the expression

$$\frac{\eta_w}{\left(\frac{t_1 \, t_2}{t_1 + t_2}\right)_w}$$

as obtained from measurements of the times of flow of pure water
 the viscometer. The value of η_w was taken by Farrow as 0.00407
 absolute units by interpolating from the data of Thorpe and
odger.

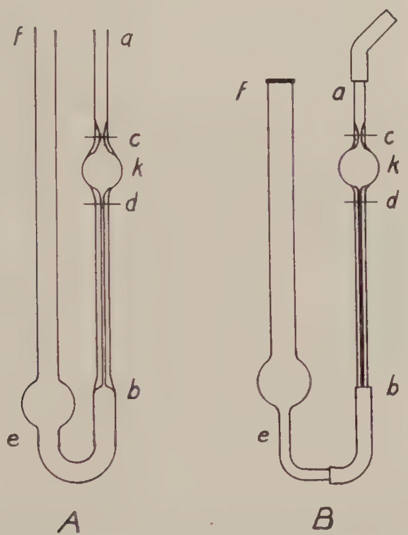


FIG. 182. Ostwald (639) tube for measuring viscosity of fluids

Viscosity changes rapidly with temperature, on the average about
 per cent per degree. The temperature must therefore be kept very
onstant, best by means of a water bath. Dust and suspended parti-
les which were so troublesome to the earlier observers who used
arrow horizontal tubes, have little effect in Farrow's apparatus
xcept in extreme cases.

A suitable apparatus which Ostwald designed is shown in figure
82. The liquid flows under its own pressure through the capillary
d. An accurately known quantity is introduced at *f*, and sucked up
t *a* until the liquid has risen above the mark *c*. The time occupied

by the liquid in flowing down from c to the lower mark d is noted. If t_o is the time for the standard liquid, whose specific gravity is s_o and coefficient of viscosity η_o, the corresponding values for any other liquid are related to them as follows:

$$\eta : \eta_o = st : s_o t_o, \text{ or } \eta = \eta_o \frac{st}{s_o t_o}$$

where we put for η_o the absolute value determined in some other way; or, if only relative numbers are needed, we make it equal to 1. A stop watch is essential in taking the time. The capillary tube should be 10 to 12 cm. long, and the bulb k so large that the time of outflow is at least 100 seconds.

For simple comparative measurements, an Ostwald tube may be improvised from a chloride tube and broken thermometer. Professor Ludwig Scheuring, of the University of Munich, states in a personal communication that such tubes are sufficiently accurate to use in ascertaining the desirability of making careful determinations.

III. CURRENT (268, 329)

A. *Effects*

Current in water is of much importance to animals in various ways. The behavior and house building relations have been touched upon in Chapter III. In addition there are many other relations, chiefly inferred, from the facts of distribution. Fresh-water sponges (149), mussels and other Mollusca show growth forms which are correlated with size of streams and with current. In the sea, tidal currents and wave action (and undertow) are also correlatable with the size of barnacles, sea mussels, corals and Littorina.

Currents are responsible for the conditions of chemical content, food, and suspension of detritus of all sorts. There is ordinarily no question as to importance of measuring them from this view point.

Currents have pronounced effects upon the migration of fishes. It has long been known (163) that the fishes belonging to the larger streams migrate up the smaller tributaries during flood periods. Snails such as Pleurocera have also been observed by the writer to move up stream during flood periods. See pages 74–80.

B. Measurement

The current in a stream, for example, is determined by the slope f the bed and the volume of water flowing. The current is swiftest t the top in the center, weaker at the bottom, and weakest at the ottom near the shore, when the stream is essentially straight. When inuate, the relations are modified. It is necessary to measure the urrent which influences the animals in their normal habitat. The nethods must be varied according to the needs of the case investi-ated. The pitot tube of Clemens is best for small streams and the ottom; Thrupp's method is good for the surface, and current meters re desirable for larger streams and mid-depths.

1. Thrupp's method. An ingenious method of obtaining the sur-ace velocity at various points in the cross-section of a stream was escribed by Thrupp (899). This depends upon the fact that if a mall obstruction cuts the surface of a stream, ripples are formed if he velocity exceeds about 23 cm. per second, while the angle of ivergence of these ripples appears to bear a definite relation to the urface velocity. To overcome the difficulty of accurately measuring his angle Thrupp constructed a velocity meter consisting of two ertical pegs (3 mm. iron nails) at a known distance d cm. apart, ith a scale measuring the distance from the base line to the point of ntersection of the ripples formed. Calling this distance L (fig. 183), he following equations were found to give the surface velocity in neters per second.

$$\text{For } d = 15 \text{ cm.}, \ v = 0.1219 + 0.0247\ L$$

$$\text{For } d = 10 \text{ cm.}, \ v = 0.1219 + 0.0336\ L$$

With d = 15 cm. and with a velocity of 0.25 meters per second he value of L is about 5 cm., while with a velocity of 1.06 meters er second, L is 38 cm.

This method would appear to be capable of results at least as ccurate as those obtained by the use of surface floats, and possibly nore so because of the greater possibilities of accuracy in the deter-nination of the area of the stream at one definite cross-section.

2. Pitot tube. A pitot tube, shown in figure 184, was used by W. A. Clemens in his work on Chirotenetes in 1917 (171). This consists f two copper tubes 60 cm. long and 3 mm. in diameter, fastened

together and having the lower ends bent at right angles so that the openings extend in opposite directions. The copper tubes are connected, by means of rubber tubing 150 cm. in length and 6 mm. in

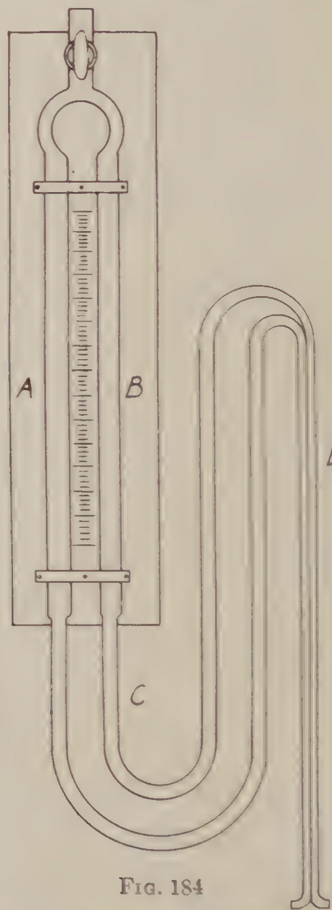


FIG. 183 FIG. 184

FIG. 183. Method of obtaining surface velocity at various points in the cross section of a stream (899).

FIG. 184. Pitot tube used by W. A. Clemens (171) in his work on Chirotenetes.

diameter, to two glass tubes each 60 cm. in length and 15 mm. in diameter. The glass tubes are attached to a board and between

them is placed a scale. The glass U-tubes are half filled with water through the copper tubes. The cock at the center is then closed, so as to make possible a differential reading of the difference of pressure in the two openings. When placed under water with one copper tube facing the current, the reading is proportional to the force of the current. This instrument was calibrated in the canal of the Hydraulic Laboratory of Cornell University.

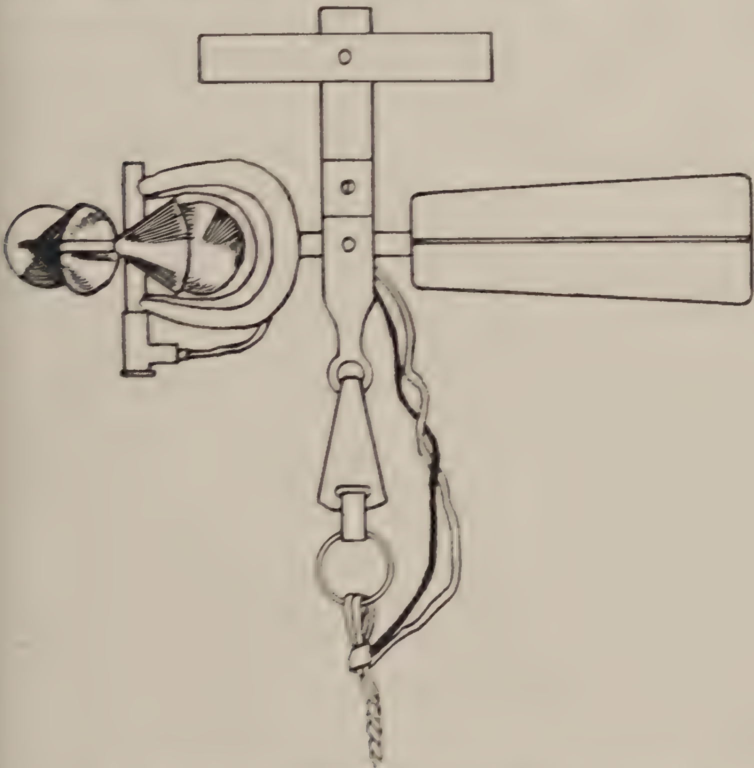


FIG. 185. Price meter for indicating flow of current

3. Current meters. The Price meter (fig. 185) is fitted with a guide vane which keeps its axis perpendicular to the direction of the current. The wheel may be either geared to a counter which records the revolutions direct and is put into and out of gear by means of a cord from the point of suspension of the meter, or may make and break

the contact in an electrical circuit at each revolution, thus enabling the number of revolutions to be indicated by means of a counter or buzzer placed on shore or in a boat. The advantages of the latter method in reducing the resistance to rotation and the tendency to clog are obvious, and the mechanically operated meter is becoming obsolete.

The instrument is previously calibrated by towing at known velocities through still water, the number of revolutions corresponding to these velocities being recorded. It has the disadvantages that it cannot be used where floating grass or weed is prevalent, and that it requires rating at frequent intervals. Further, it cannot be used at very low velocities. The minimum permissible velocity depends on the type of meter, but in general varies from 8 to 15 cm. per second.

IV. SURFACE TENSION

Theinemann's "fauna hygropetrica" (149) clings by surface tension in that thin film of water which surrounds the surface of stones not truly submerged. Some animals live on the surface film, e.g., water striders, or hang below it as do insects, snails, entomostraca and flat worms. Some small animals, such as ostracods, occasionally break through the surface film and cannot get into the water again.

The importance of surface tension has been shown recently in the artificial cultivation of various bacteria (510). Its importance is also being recognized in the effectiveness of various insecticides. For example, the adhesiveness and spreading quality are greatly increased in a solution of lead arsenate by the addition of a colloid. The killing effects of nicotine sulphate and many of the oils are greatly increased by a reduction of the surface tension by the addition of soap. (Metcalf and Flint (593a).)

1. Methods of Measuring

a. Drop method. The most simple method of determining surface tension is the drop method. The formula follows:

$$\frac{\text{Weight of fixed number of drops of solution}}{\text{Weight of fixed number of drops of water}} \times 73$$

where 73 = the surface tension of water.

This method is doubtless not accurate, but probably sufficiently so for the purposes of determining whether further work should be done. The glassware must be scrupulously clean, and either the same pipette or preferably two pipettes of the same size should be used. This method is refined enough for preliminary work and has been used in the writer's laboratory in connection with insecticides. Elaborate glassware for use in this method may be purchased. Drop number and surface tension were used by Adams, Burnett, Jenkins and Dreger (9) in a piece of work on the anaesthetic action of a series of alkyl paraminobenzoates in which the writer assisted in the use of the goldfish as a test animal. There was a striking correlation between both these determinations and the index of anaesthesia; this was especially striking in the case of surface tension.

A somewhat more accurate method which can be used for any liquid which will wet the glass tubing (cannot be used for such substances as mercury) consists of a glass tube of small bore, held vertically with the lower end in the liquid. A scale alongside measures the capillary rise. The surface tension can then be determined by the following formula:

$$T = \frac{Rhdg}{2}$$

where T = surface tension in dynes per centimeter
d = density of liquid
h = height to which it rises
R = radius of the tube
g = gravity = 981

To carry out the experiment the glass tubing is thoroughly cleaned and washed out with the liquid. A new tube should be used for each substance. Density may be found with a specific gravity bottle.

Another apparatus extensively used is the Du Nouy precision tensiometer (Central Scientific Company). A platinum wire ring is lifted through the surface film and the torsion of a slender steel wire is used to indicate the breaking strength of the film which is readily converted into surface tension. It is often desirable to determine the surface tension of body fluids, sperm suspensions and protoplasm itself.

V. HYDROSTATIC PRESSURE

Hydrostatic pressure within one to two atmospheres has little effect on most animals. The effects of enormous pressures were

observed by Regnard (719), who increased hydrostatic pressure to several hundred atmospheres, securing effects in carp, salmon egg, Paramoecia, etc. Protoplasm takes in water under high pressure.

VI. OSMOTIC PRESSURE (43)

The osmotic pressure of fresh water is usually not great. Some salt lakes and the sea have relatively large osmotic pressure.

There is a great difference in the osmotic pressure relationships of plants and animals, though in the most primitive groups there is little difference. The ontogeny of forms being a recapitulation of their phylogeny morphologically, it is none the less true that in physiology we have a similar relationship of which osmotic pressure is an expression (43).

The osmotic pressure depends upon the number of ions and molecules in a definite weight of solvent; hence it is evident that the pressure within a living cell is regulated by the activity of the cell protoplasm in synthesizing colloidal matter from crystalloids and in splitting up colloids again to form crystalloids together with the entrance of external ions and molecules, the entrance of which is governed by the variations in permeability of the protoplasmic membrane.

1. *Osmotic pressure in animals* (291)

The substance of the following summary is taken largely from an article by Atkins (43) and others (325, 605, 869).

The osmotic pressures in plants can be raised to remarkable heights, since here the internal tension is taken up by the strong and supporting cell wall (425). In animals, on the other hand, this is not possible and the osmotic pressure cannot rise a great deal above that of the surrounding medium, for the increased pressure would burst the cell.

a. The lower water-dwelling animals. In all these there is more or less complete contact between the organism and the medium, and the excretory system serves to adjust the osmotic pressure. The osmotic pressure is equal to or slightly above that of the water in which they live and the excess is sufficient to maintain the turgescence. Thus the same species in the Bay of Naples may have a higher osmotic pressure than in the Atlantic.

b. Fishes (43, 324, 869). The cartilaginous fishes communicate freely by their gill membranes with the water, and are capable only

of passing from sea water to brackish estuaries. In this case the blood and body salts or the total weight undergo a change to bring the animal into equilibrium with its surroundings. The teleosts (43) on the other hand, possess gill membranes that are largely impermeable to salts (1006), and here we have a mean value of osmotic pressure, but this may change somewhat in the changing salinity. In the anadromous fish (43) like the salmon the impermeability is of a very high order, as they can pass from the sea with a pressure of about 24 atmospheres to the fresh at 0.25 while maintaining approximately the normal pressure which varies with the species from 7.2 to 10.8. The eggs (43) which are laid in the fresh water thus will in all probability change in their osmotic pressure from that of near fresh water to that of the mature fish.

Sumner's (869) finding may be summarized as follows: (1) Certain brackish and salt water fishes were unable to survive even a gradual transfer to pure fresh water, though enduring an abrupt transfer to water of a very low degree of salinity. The fresh water as such proved fatal. The degree of abruptness of the change was of secondary importance. Abrasions of the surface of the fishes did not seem to influence the situation materially.

(2) Considerable changes of weight were found to result in many cases from changes in salinity (hence osmotic pressure) of the surrounding medium. In *Fundulus heteroclitus*, the body fluid of the fishes used had an osmotic pressure of water of the density of 1.005 to 1.015. Transfer to one decidedly hypotonic resulted in gain in weight, the osmotic pressure being raised, and *vice versa*. In no case was osmotic equilibrium between the internal and external medium established. The osmotic pressure within the organism fluctuated within much narrower range than that of the water. The change in weight bore no constant ratio to the change in osmotic pressure of the water, the greater changes in weight occurring where the change was harmful. Scraping off the scales did not result in changing the influx or efflux of water.

(3) Considerable changes in the salt (chlorine) content of the body were likewise found to result, in many cases, from changes in the salinity of the water (in some cases there being a loss at first with a subsequent gain, in others a continuous loss).

(4) Careful control experiments excluded the possibility that the water or salts entered or passed from the body through the alimentary

canal, leaving only probable alternative an osmotic exchange through one or more of the limiting membranes.

(5) In certain fishes, at least, it was found that the membranes chiefly concerned in such exchanges were those of the gills. (This experiment was carried on with a carp which with its body in fresh water and salt water pouring over gills lost 6 per cent in five hours; when with body in salt water and fresh water pouring over gills no change in weight occurred.)

In general the conditions seem impossible to state in advance for a given case, nor are the changes at all proportional to the changes in the density of the external medium.

c. Reptiles (43). Little investigation has been done in this group but each species has an approximately constant osmotic pressure. Some fresh water forms have a pressure of about 5, while some of the marine species will go to 7 atmospheres. The fact is pointed out that the blood of fresh water forms is approximately isotonic with that of the cells in the eggs of birds.

d. Amphibia (43). The frog has been the subject of a great deal of research along this line and the osmotic pressure of its blood is about 5.5 atmospheres. A gradual increase in osmotic pressure from spawn up to maturity has been traced. The osmotic pressure here as in all classes from the teleosts upward is delicately regulated by the nephritic system.

e. Birds (43). The osmotic pressure of birds is characteristic for the species and is higher than that of reptiles or amphibia, being about 7.2 atmospheres. The osmotic pressure of fresh eggs is constant and about 5 to 5.5 atmospheres. The osmotic pressure increases progressively with growth and is no doubt the result of the splitting of colloidal molecules.

f. Mammals (43). The fluids in this group have been investigated thoroughly, particularly those of physiological importance, notably the blood, milk and urine. As a whole the freezing point of the group lies between $-0.55°$ and $-0.6°$C. (6.6 to 7.2 atmospheres) and is remarkably constant. In man the normal for the blood is $-0.56°$C and may vary ± 0.01 in health. In health the urine ranges from $-0.9°$C. to $-2.1°$C. The milk is also remarkably constant and gives a value a little lower than that of the blood; that of the cow lies at $-0.55°$C.; variations exceeding 0.02 are rare.

g. Summary (43). On the whole the osmotic pressure of anima

ells does not exceed ordinarily 7.5 atmospheres except those that ive in the sea where it only slightly exceeds that of the medium. If ower than that it is because its membranes are more or less imperneable and thus render it independent of the surroundings to some xtent. Within the body each cell must be thought of as a water lweller, being in osmotic equilibrium with all the cells in the body nd with the intercellular solutions.

2. Methods of measuring osmotic pressure (747)

a. Plasmolysis (43). The use of the plasmolysis method in the letermination of the osmotic pressure has the disadvantages that it ;ives a value that is a little too high, as the solution has to cause a hrinkage of the cell to its normal limits due to the overcoming of the nternal pressure, before plasmolysis takes place; also that the memorane is seldom completely impervious to the solute in the external nedium and the permeability changes and even the external soluion may change this. For these reasons the freezing point method is uperior if care is taken to get sufficient quantity of the juices and o have them experimented upon before any changes can take place.

b. Depression of freezing. This consists merely in determining the emperature at which the fluid freezes. The depression below the reezing point of pure water bears a direct ratio to the osmotic pressure. Formerly it was supposed that osmotic pressure could be alculated from the results obtained from the determination of the reezing point of weak solutions of nonelectrolytes such as N/20 sugar olutions, but the law of correspondence of gas and osmotic pressure loes not hold generally (372). Accordingly it is best to use the able of osmotic pressures accompanying different freezing points in arious textbooks of plant and animal physiology or biochemistry 584).

One of the most practical methods of determining temperatures n small amounts of fluid and in small cavities, or wherever space is imited, is with thermocouples. These, however, have commonly been elatively little used, largely because of the complication of the pparatus, its delicacy and the fact that one constant temperature as ordinarily to be maintained. Robinson (742) has recently decribed the method quite fully, as used at the University of Minnesota vhere it has been employed in determining the freezing points of the ody fluids of insects in situ (the depression of the freezing point

below 0°C. may be used to secure the osmotic pressure). The method described by Robinson requires a thermos bottle of ice and water, a pyrovolter and outside galvanometer. Thermocouples are made by twisting fine copper and constantan wire together and dipping the junction into melted solder; the sensitive point is at the first contact of the two metals at the base rather than the tip of the coiled

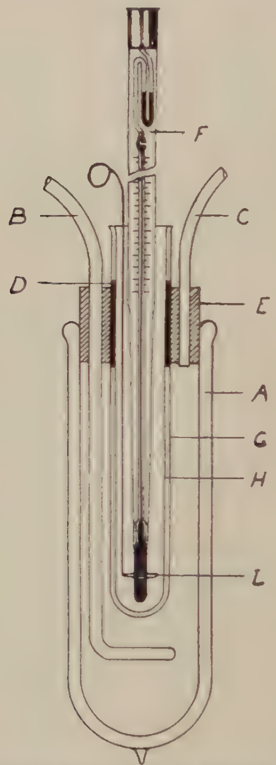


FIG. 186. Apparatus for determining the freezing point of blood, vegetable saps, milk, and other animal juices (after Bartley, from Mathews (584)).

portion. Robinson gives full instructions and many important hints as to the use of his method.

The Leeds & Northrup Company can supply a potentiometer with a nickle or platinum coil the resistance of which changes with temperature so that the cold junction is dispensed with. They also can supply a potentiometer which may be used in the field with a Rawson unipivot galvanometer and no other accessories.

A convenient form of apparatus for determining the freezing point of blood, vegetable saps, milk or other animal juices is that shown in figure 186, described by Bartley. The apparatus consists of a Dewar tube, A, 22 cm. high and 6 cm. inside diameter, set in a wooden base. This is fitted with a rubber stopper, E, having three holes. Into the large hole is fitted a heavy glass test tube, G, 20 cm. long and 3 cm. wide passing down to near the bottom of the vessel A. Two other holes are for small brass or copper tubes, one, C, terminating just below the rubber stopper and the other, B, passing to the bottom of A and coiled around two or three times. These coils are perforated with a series of small holes. Inside of the test tube passing through the rubber stopper is a second test tube, H, of about the same length and 2.5 cm. in diameter, held in place by a section of rubber tubing, D, drawn over it and separating the two tubes by a narrow space. In operation this space is filled with alcohol. A delicate thermometer, F, with a platinum wire, L, coiled loosely around its lower end, completes the apparatus.

To use the apparatus, fill the tube A about one-third full of ether or carbon disulphide. Insert the rubber stopper, E, tightly, connect the shorter metal tube with a Richard's aspirator pump, attached to the water service. The liquid to be frozen is placed in the inner test tube, H. There should be enough liquid to cover the mercury bulb of the thermometer, when the latter is lowered to the bottom of the tube. The water is then started through the Richards aspirator pump which draws air through the ether in a series of bubbles, causing it to evaporate.

Owing to the well-known principle of the Dewar tube, applied in the popular thermos bottle, almost all the heat used to vaporize the ether is derived from the thin layer of alcohol between the two test tubes and from the liquid under examination. There is no frosting of the outer vessel, the whole system remains clear and transparent and the thermometer can easily be read at all times.

When the temperature reaches zero, the stirrer, L, is used. It will be observed that the temperature steadily sinks to $-2°$C. to $-3°$C. before freezing begins, i.e., 2° or more below the true freezing point of the liquid. Then, suddenly, freezing occurs and the temperature reading rises to a fixed point and remains there for some minutes. When this point is reached the water is shut off and an accurate reading taken. This is the freezing point of the liquid. There is no

necessity of adding ice to start the freezing, as is usually done in other forms of apparatus. The whole process is automatic and all the observer need do is to regulate the flow of water running through the pump and read the thermometer. It is advisable, when the temperature reaches zero, to draw the air through the ether more slowly until freezing takes place, by partly shutting off the flow of water. For accurate work the Beckman adjustable thermometer should be used. The thermometer is the most important and most expensive part of the apparatus.

VII. PERMEABILITY (359, 634–638, 374)

Permeability goes hand in hand with osmotic pressure and its regulation. This is made very evident from the preceding discussion. The tests of permeability often go hand in hand with those of osmotic pressure. Some other tests are however of a different character.

Bethe (81) found that neutral red could be introduced into cells as an indicator in the study of permeability. Warburg (941) in his work on the permeability of sea urchin eggs to alkalies, made use of this dye in staining the cells. Harvey (374, 375) in his studies on the penetration of cells to alkalies found it difficult to secure animals whose cells contain a pigment that shows a marked color change on addition of alkali. In the absence of a suitable pigment he introduced neutral red into the cells, a method which has been criticized recently (555) but which Harvey (374, 375) has shown to be unaffected by proteins, lecithin, etc., in respect to sensitivity to different alkalies. It was found (375) that living cells would not stand staining with indicators of acids (as has been done previously for alkalies), so that organisms with natural pigment had to be found. Though many pigmented animals are known to occur, those containing suitable indicators are quite rare.

While on the Barrier Reef expedition, Harvey obtained *Stichopus ananas*, the "prickly fish," which contains a natural indicator. The pigmented testis of this form served as materials for his study of the speed of acid penetration of protoplasm. Crozier (218) at the Bermuda Biological Station, found *Chromodoris zebra*, a nudibranch, containing a suitable indicator, which he utilized in studying the penetration of acids. Further investigations at Bermuda have enabled Crozier (219) to describe the color changes of indicators

derived from four pigmented animals, showing that natural indicators in animals are not quite so rare as had previously been supposed. As investigators have found it necessary to go to a considerable distance to secure naturally pigmented animals suitable for such studies, it seems very desirable to ascertain whether plant tissues suitable for such studies are not readily available.

It is further desirable to investigate dyes that may be used to impregnate animals in vitro.

VIII. ELECTRIC CONDUCTIVITY

It is often desirable to determine the electric conductivity of natural waters. Evershed and Vigrioles, Ltd., of London, sell a hand-operated apparatus for this purpose which can be carried in the field. The conductivity of the water is determined by the dissolved electrolytes and is directly proportional to their concentration. Wells used this method to determine the character of the gradient in the water gradient tank (963). There are numerous dip conductivity cells on the market which may be used to insert into natural waters and various other cells that may be used for small quantities of fluid. Leeds and Northrup make a compact apparatus for this purpose Electric conductivity may be continuously recorded as an indication of salt content.

IX. TEMPERATURE

1. *Effects*

The effect of temperature on the rate of growth of aquatic animals is similar to that of other animals. The threshold is similar in position relative to the straight line limits, and the velocity falls off at high temperature as shown in figures 65–73 and discussed in Chapter VII. The velocity curves are shifted down the scale of temperature. The threshold of the mealworm pupa is approximately 10°C. while that of the European frog embryo is approximately 7°C. (423).

Reactions to temperature are discussed in Chapter III. The selection of lower temperature at stream junctions by the sockeye salmon emphasizes the numerous correlations pointed out especially for marine animals, as is well illustrated by reports on expeditions of the Michael Sars (610). There are also numerous structural characters correlated with surrounding temperature, and in a few cases experimentally structural modification have been demonstrated.

2. Control and measurement (868)

The control of temperature in water has been regarded as a single factor process in too many cases. When the temperature of water is changed, most of the chemical and physical conditions are disturbed. The solubility of gases varies with temperature. It is then necessary for most purposes, to allow the water being warmed or cooled to come into equilibrium with the air before it is used on animals. The thermostat should be in the water in which the animals are kept; the heat or cold should be applied in an open vessel while the water is being agitated. If warmed under pressure the excess nitrogen may cause gas bubble disease in animals. (See p. 522.)

In regulating temperature the use of hot and cold water with a mixing valve under thermostatic control is not a desirable method of controlling water temperature. It requires a separate vessel (or section of the aquarium) in which the water may be stirred with fans or bubbles of compressed air. Otherwise the temperature fluctuates rhythmically. The energy used in the heating or cooling of the two kinds of water is largely wasted in securing bad results. Any apparatus for directly heating water in standing aquaria should include apparatus by which the water may be stirred continuously.

CHAPTER XVIII

Light Conditions in Water

I. Introduction

Correlations between the abundance of plants and the absorption of light with depth in water have long been made. Gail correlated the occurrence of algae and diatoms with observations of Shelford and Gail (830) on light penetration into sea water. He further studied optimum light for photosynthesis in various plants. Although plants do not appear to dominate the sea or its bottom they have important relations to the bottom and pelagic fauna. The influence of plankton algae is important in fresh water, and there is no doubt of the importance of light and its penetration from this view point. Correlations between the quantity of various species and light duration have commonly been noted. E. J. Allen (23) correlated mackerel production and sunshine. Kofoid (486, 487) correlated some of the phenomena of the Illinois River plankton with the light of the moon. Correlation of plankton pulses with more or less sunshine has been frequently suggested.

From the standpoint of growth (850), behavior, migration, and distribution, correlations with night and day, cloudiness, latitude, turbidity, etc., are so familiar that it is unnecessary to do more than cite a few papers whose bibliography will lead the reader further into the field (23, 246, 283, 284, 422, 610, 778).

II. LIGHT CONDITIONS IN WATER

The selective absorption of different wave lengths by water (354, 480, 483, 610, 678) is familiar (fig. 187). The effects of turbidity are well known, and only a few details can be taken into account here.

1. Pure water transmission

Absorption is commonly expressed as a coefficient of absorption for one meter.

This is the reciprocal value of the thickness of a stratum of water which would reduce the intensity of the transmitted light to the fraction of $\frac{1}{2.7138}$ of

its value at entrance. The number 2.7183 is the basis of the natural system of logarithms and the value of the fraction is approximately 0.37. This coeffi-

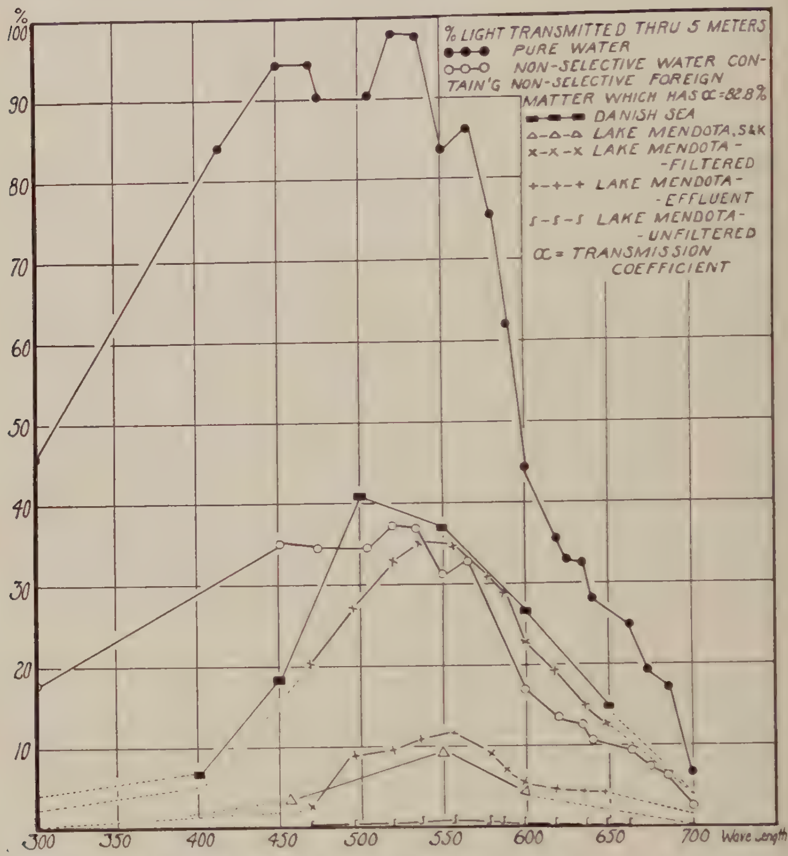


FIG. 187. Showing the light transmitted through 5 meters of the various waters indicated. The pure water is calculated from Pietenpol (678, table 1, p. 571). The curve for non-selective water with non-selective foreign matter is calculated for Puget Sound water as read with the Kunz photoelectric cell (827). Selective effects of the water were not determined. The Danish sea water curve is calculated from Knudsen's (483) data obtained with a sub-aquatic spectrophotometer using photographic plates. The Lake Mendota "filtered" shows the effect of dissolved stains. The "effluent" shows the effect of dissolved stains and part of the suspended matter left in by a centrifuge. The "unfiltered" water was taken beneath the surface where the amount of suspended matter is much greater than at the surface and makes the calculated values too low. The curve marked by triangles is from measurements with three photoelectric cells with screens (by Shelford and Kunz (831)). The dotted line extensions are mere estimates based on pure water.

TABLE 47

*Showing transmission of light of different wave lengths by pure water (transmission coefficients)**

WAVE LENGTH†	PER CENT TRANSMITTED TO DEPTHS NOTED						
	1 cm.	1M.	5M.	20M.	25M.	35M.	50M.
		(Exponents)	(1^5)	(5^4)	(5^5)	(5^7)	(25^2)
$\mu\mu$							
186.0, Sm	54.40	3.63×10^{-25}					
193.0, Sm	98.37	19.33					
200.0, Sm	99.10	40.50					
210.0, Sm	99.39	54.24					
220.0, Sm	99.43	56.46					
230.0, Sm	99.66	71.14					
240.0, Sm	99.68	72.58					
260.0, Sm	99.75	77.88	28.65	0.673	0.193	0.015	3.72×10^{-6}
300.0, Sm	99.85	86.07	47.23	4.97	2.352	0.525	0.055
415.0, E	99.96	96.59	84.0	49.9	42.0	29.0	17.6
420.0, E	99.97	97.74					
449.0, E	99.98	98.81	94.2	78.7	74.1	65.8	54.9
450.0, A	99.98	98.03					
468.0, E	99.99	98.81	94.2	78.7	74.1	65.8	54.9
470.0, P	99.96	96.67					
475.0, A	99.98	98.03	90.5	67.1	60.8	49.8	37.1
494.0, P	99.97	97.06					
506.0, A	99.98	98.03	90.5	67.1	60.8	49.8	37.1
510.0, A	99.97	97.54					
522.0, A	99.98	98.52	97.8	74.2	68.8	59.3	47.4
525.0, A	99.97	97.06					
537.0, A	99.99	99.50	97.5	90.5	88.2	83.9	77.8
539.0, P	99.98	97.93					
550.0, A	99.97	96.48	83.6	48.8	40.8	28.5	16.6
558.0, P	99.97	96.48					
562.0, A	99.97	97.06	86.1	55.1	47.4	35.3	22.5
575.0, A	99.98	98.03					
579.0, P	99.93	94.59	75.7	32.8	24.8	14.3	6.1
587.0, A	99.95	95.06					
589.5, P	99.90	90.90	62.0	14.8	9.19	3.5	0.85
600.0, A	99.84	85.04					
600.5, P	99.83	84.87	44.0	3.76	1.6	0.32	0.027
610.2, A	99.81	82.68					
618.0, P	99.80	81.48	35.9	1.6	0.59	0.077	0.0035
625.0, A	99.78	80.10	32.9	1.18	0.39	0.0429	0.0015
636.0, P	99.77	79.96	32.6	1.14	0.38	0.0396	0.0013
637.0, A	99.77	79.65					

TABLE 47—*Continued*

WAVE LENGTH†	PER CENT TRANSMITTED TO DEPTHS NOTED						
	1 cm.	1M.	5M.	20M.	25M.	35M.	50M.
		(Exponents)	(1^5)	(5^4)	(5^5)	(5^7)	(25^2)
$\mu\mu$							
640.0, A	99.75	77.61	28 0	0 627	0.18	0.014	0 00013
650.0, P	99.76	78.68					
662.0, A	99.72	75.64	24.7	0.37	0 09	0.0056	$8\ 06\times10^{-8}$
663.0, P	99.76	78.40					
675.0, A	99.67	72.10	19.48	0.141	0.028		
687.0, A	99.65	70.35	17.23	0.088	0.0151	2.31×10^{-6}	
700.0, A	99.45	57.83	6.4	0.00167	0.000107		
779.0, Sm	76.18	1.54×10^{-10}					

* Calculated from coefficients by authors, or from the sources designated by letters: A, Aschkmass; P, Pietenpol; E, Ewan, Sm, Smithsonian physical tables. The data by Aschkmass and by Ewan are from Pietenpol.

† Wave lengths correspond to colors as follows: 300 and less, ultraviolet; 415, violet; 420–506, blue; 510–525, green; 537–589.5, yellow; 600–640, orange; 650–700, red; 779, infra red.

cient may be stated in terms of any desired unit of measure for the thickness of the stratum. In this case the meter is employed. An absorption coefficient of unity, therefore, means that a stratum of water whose thickness is unity (1.000 meter) absorbs so much light that the intensity of the transmitted light is equal to 0.37 of its original value. An absorption coefficient of 0.200 means that if the rays of light were passed through a layer of water 5 meters thick ($\frac{1.000}{0.200}$) its intensity would be reduced to 0.37 of its original value. Similarly a coefficient of 1.250 would mean that 0.80 meters would reduce the intensity of transmitted light to 0.37 of its original value. For the purposes of this kind of investigation the results might as well be stated in terms of the percentage of the transmission of light by a meter of water as in those of the coefficient of absorption. The absorption coefficient method is regularly used by physicists and is of advantage in certain types of computation. (Pietenpol, 1918).

Coefficients of transmission are advantageous, easily calculated while working and are accordingly used. Table 47 was calculated from the Smithsonian Tables (852) and Pietenpol's (786) table of absorption coefficients.

2. Refractive index

Using the refractive index of water, an attempt was made to determine the approximate angle which the light rays took or would take

f the water surface were smooth. It is the opinion of several physicists consulted, that with the entire water surface flooded with light, such an assumption is the only one that can be made. The waters about Friday Harbor are remarkably smooth and only the smoothest days were used. The refraction of the water tends to bend the light to a more nearly vertical direction. Figure 189

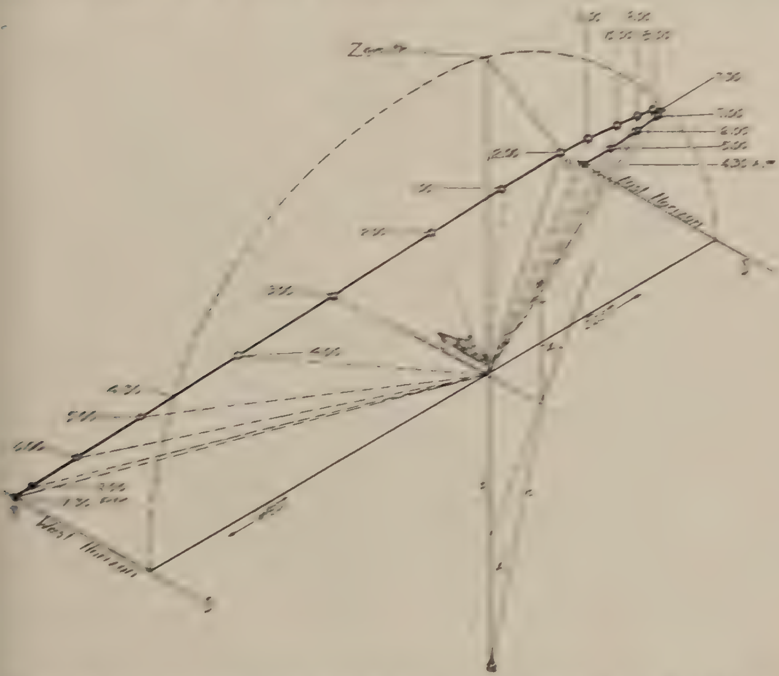


FIG. 189. Showing the path of the sun (heavy line with small circles) on August 1, 1925 at Friday Harbor, Washington (527). The angle corresponding to A must be determined and the value of A′ and the distance c calculated for all readings.

shows the relations of the sun to the water surface at the different hours. The refracted path of a ray of light is shown with appropriate lettering. In calculating the angles, a table of natural sines and cosines is needed. The refractory index of water is about 1.333, which means that $\frac{\sin A}{\sin A'} = 1.333$ (see fig. 188). It follows that A' is an angle whose sine is three-fourths the sine of A. To make use of the

table of natural sines it is well to bear in mind that in the case of a right triangle, $\sin A = \cos (90 - A)$, and $\cos A = \sin (90 - A)$. In the calculation of the light path per meter of depth, the fact that $\cos A' = \frac{b}{c}$ was used and b taken to equal 1 meter vertical and c the oblique distance (fig. 188). Hence $c (\cos A') = 1$, or $c = \frac{1}{\cos A'}$.

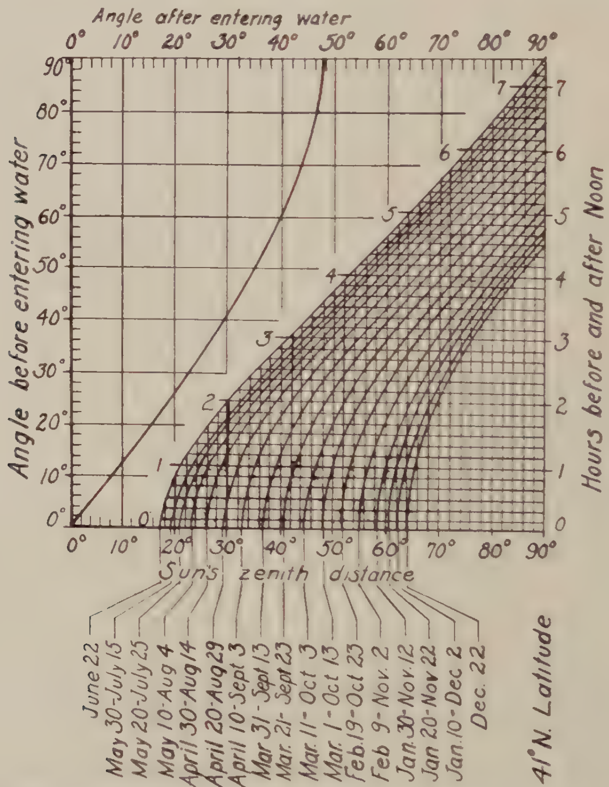


FIG. 189. Showing the sun's zenith distance on different days and hours of the year at 41° North latitude, (Modified from Clements (173)) with a curve showing the angle of light before and after entering water.

Some typical and average results are shown in table 48, in which the location, date, sun time, and sun's zenith distance or deviation of the light rays from the perpendicular are shown. It is best to prepare a chart such as shown in figure 189 for the locality of study. The

sun's zenith distance for each hour and for a series of dates about ten days apart is sufficient. The chart should show deviation from perpendicular before and after entering water. A single curve showing the angles before and after entering water is sufficient. The sun's zenith distance may be ascertained at the time of light observation with a sextant or, roughly, with a shadow post, and protractor and plumb line, or from tables (913, 914) of the sun's elevation. On an unstable boat this last method is likely to give very rough results. The sun's zenith distance may also be ascertained by using a celestial sphere set for any locality.

3. Natural waters (610, 621, 781, 782, 827, 830, 831)

a. Vertical penetration. The penetration of light into natural waters is governed by suspended matter, surface disturbance, and staining.

Average light conditions in water are more affected by amount of suspended matter, such as silt and plankton organisms, than by anything else. Many rivers have only a very small penetration especially during flood periods. Light penetration is impeded in many otherwise clear lakes and streams by plankton, especially in the summer months. The seas are usually clearest. In Lake Mendota the per cent of blue light at 5 meters is about the same as at 35 meters in Puget Sound.

Suspended matter in the form of earthy materials and organic detritus, was thought to be nonselective as to color or wave length in Wisconsin Lakes. This, however, can hardly be generally true, as much green plankton sometimes occurs and chlorophyll is decidedly selective. Figure 187 shows, in the curve with triangles, that the water of Lake Mendota absorbs light selectively. Comparison between Dolphin Bay (fig. 192) where the water was green with diatoms, and the average for San Juan Channel demonstrates the same thing. The violet in Dolphin Bay at 5 meters was about one-fifteenth that in the Channel. The short-dash curve shows what the entire series should be for Dolphin Bay if the 1:15 ratio were correct throughout; whereas the blue was actually nearly twice as intense and the green and yellow four times. Again figure 190, *A* and *C*, show that Puget Sound waters are selective as to wave-length transmission and accordingly penetration cannot be considered separately from wave lengths.

b. Illumination of objects from the sides and below. Williams (975a) studied horizontal and vertical intensity of light in Puget Sound waters. Figure 190, *B*, shows this relation. The cell used by

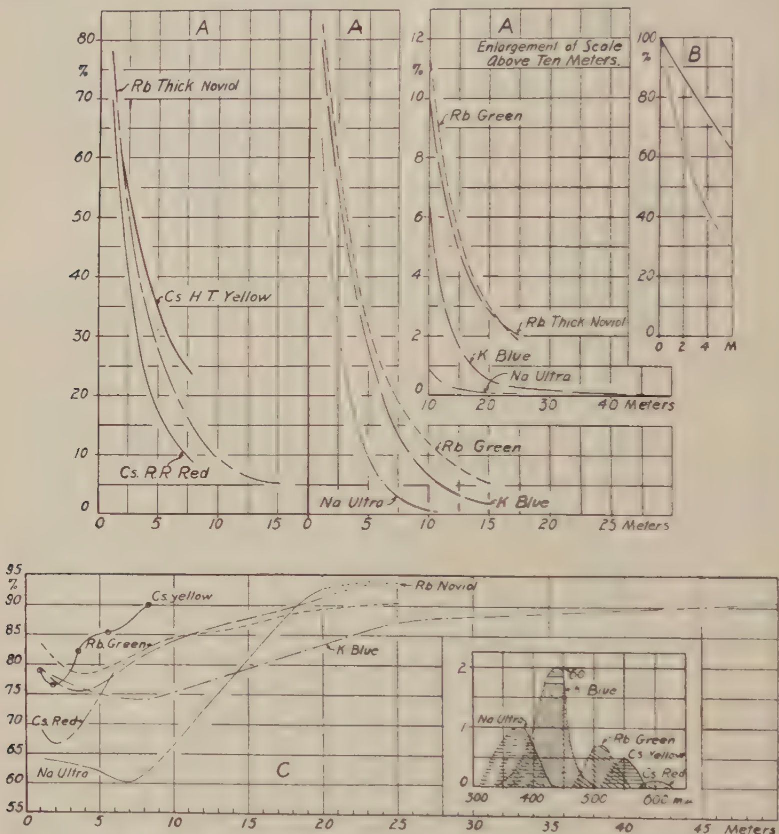
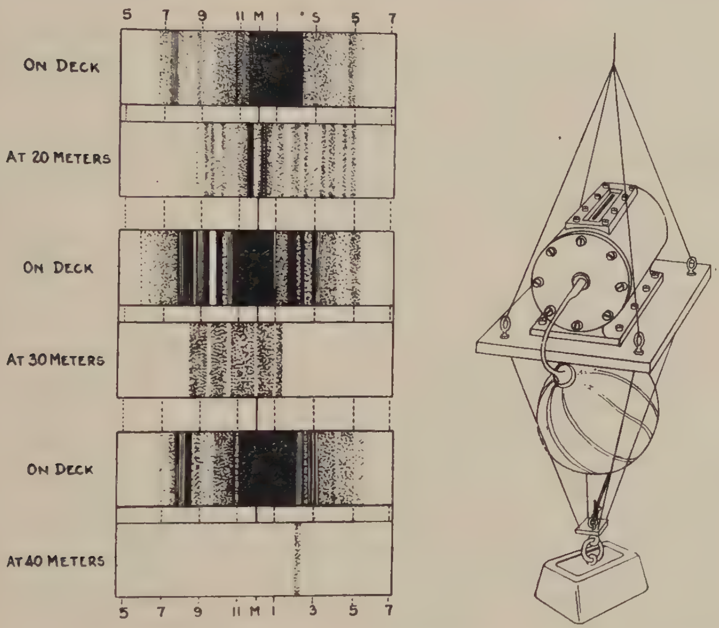


FIG. 190. *A* shows the per cent of light of different colors at different depths in San Juan Channel as measured with cells of different alkali metals screened so as to give the wave length sensitivities indicated in the lower right hand corner of *C*. *B* shows the decrease of vertical upward (right) and horizontal (left) illumination from data by Williams (975a). *C* shows the changes in per cent transmitted per meter at different depths with the cell and screen combinations shown at the right.

Williams (975a) bore a long tube so that only direct rays entered the cell. Within an hour of noon horizontal light just above the water ranged from 0.04 to 0.016 of the sunlight and the light just below the

water was 0.20 to 0.06 of that above the water depending on a considerable number of conditions. The horizontal light just below the surface is 0.008 to 0.00096 of sunlight. The light upward just below the surface is about 0.0035 of sunlight.

c. Surface conditions (827). Surface conditions greatly affect the amount of light entering the water. This probably brought about



A *B*

FIG. 191. *A* shows Regnard's (719) results from exposing the instrument hown in figure *B* at 20, 30, and 40 meters with another similar instrument on leck. The results of changes in surface conditions are probably indicated by he lack of accord in the light effect bands on the photographic paper. *B* hows Regnard's photographic paper photometer, in which the paper was urned in front of a slit by clock work. Note the rubber sack to equalize nside and outside pressures.

Regnard's peculiar results, figure 191, *A*, *B*. The large amount of ight shut out by the surface and the few centimeters to which it was necessary to submerge the cell on account of surface condition, has eemed to some quite incredible. The variation within seven minutes hown in table 48 (determined with unscreened K cell) constitutes an adequate explanation. It should be noted also that the surface

transmission changed from 67.3 per cent to 26.0 per cent in three minutes (3:14 to 3:17 p.m.) with increasing surface disturbance. When the tide is running through narrow channels, the surface is characterized by innumerable whirlpools. These are apparently crossed by wave motion, making a very complicated surface. The surface of rivers is similar, but that of lakes is probably less complicated.

Cells screened as shown in figure 190, *C*, give peculiar results in that the blue and green average 85 per cent transmitted while the

TABLE 48

Showing the effect of currents on light penetration during 7 minutes, east of Brown Island at Friday Harbor and elsewhere; the mean of columns a and b is 63.8 (830)

SURFACE	JULY 19						OTHER DATES	
	Sun time, hours, minutes	Zenith distance		Depth	m.c. light units	(a)		(b)
		Air	Water			Per cent	Angle	Surface transmission
Covered	3:10	47°		0	0		27°0	82.5
Dry	3:12	47°		0	48,300	100.0	27°5	68.5
Tide ripples	3:13	47°	33° 16′	0 wet	30,600	63.0	29°	92.0
Tide ripples	3:14	47°	33° 16′	0 wet	32,500	67.3	32°	73.0
Tide ripples	3:15	47°	33° 16′	0 wet	30,600	63.5	32°	80.0
More tide ripples	3:16	47°	33° 16′	0 wet	29,200	60.6	37°	89.0
Froth	3:17	47°	33° 16′	0 wet	12,500	26.0	37°	86.0
Strong tide rips	3:18	48°	33° 52′	0 wet	22,300	46.1	37°	33.0
Strong tide rips	3:19	48°	33° 52′	0 wet	23,200	48.7	70°	42.4

orange (caesium with red screen) and the yellow give only 73 per cent and the violet-ultraviolet (sodium) show 79 per cent transmitted by the surface. This was under clear sky and unusually smooth water at Friday Harbor, Washington. This shows an average of 79 per cent transmitted as shown by screened cells. Poole and Atkins have called attention to the possible effect of the dispersing lens of water above the spherical cell. The importance of cell form is illustrated by a few readings with a double sphere cell (fig. 137, *B*) which showed only 14 per cent transmitted. It will be noticed here that the last column of table 48 shows that when the sun is high the most common

reading is of the magnitude of 85 per cent transmitted which is about the finding of Poole and Atkins for the English Channel. The readings with the unscreened cell are probably within 5 per cent of the results of other methods and the relative results are probably essentially correct. These measurements should however be made with flat surfaces or diffusing screens.

III. SELECTIVE TRANSMISSION OF WAVE-LENGTHS; COLOR AND DEPTH

Pure water, as has already been shown, transmits various portions of the spectrum selectively. The red is absorbed very rapidly by pure water so that at 10 meters depth red objects may look black. Violet, ultraviolet, and green and yellow are absorbed to a moderate degree while blue is transmitted with little reduction.

Staining of the water by organic matter, tannic acid, etc., which is usually brown, has the effect of amber and yellow glasses. It cuts out the blue in particular. (See curve for Lake Mendota, filtered water, and for Danish Sea water, in fig. 187.)

Figure 190 shows these relations for the Puget Sound waters (827) as measured with photoelectric cells of four different metals and glass ray filters. The sensitivity of these cells is shown below, figure 190, *C*. Striking absorption of red, blue, and violet is indicated. Comparison in figure 190, *C*, shows that the water clears up rapidly to the violet and ultraviolet with increased depth.[1] Transmission is least for red and yellow at 2 meters, for green at 3.5 to 4.0 and for blue and violet, at 7 meters. No adequate explanation can be offered for the low transmission of the red and yellow near the surface. The form of the cell and surrounding casings may have had some influence. The dispersal and absorption of violet and ultraviolet light, by the fine transparent sand grains found in the water in some quantity, is a possibility suggested by the writer (827). These sand grains are found in the plankton nets and mixed in with the plankton detritus which occurs on the bottom of some large enclosed bays of San Juan Island group. The distribution and stratification of

[1] In an address before the Royal Geographic Society (404) Murray and Hjort state that violet and ultraviolet penetrate farthest, though in their book (610) they mention only blue. In the book, Wratten and Wainwright three-color-filters are mentioned. It has been impracticable to consult Hjort's account published in Bergen. Grein's (354) findings are probably correct.

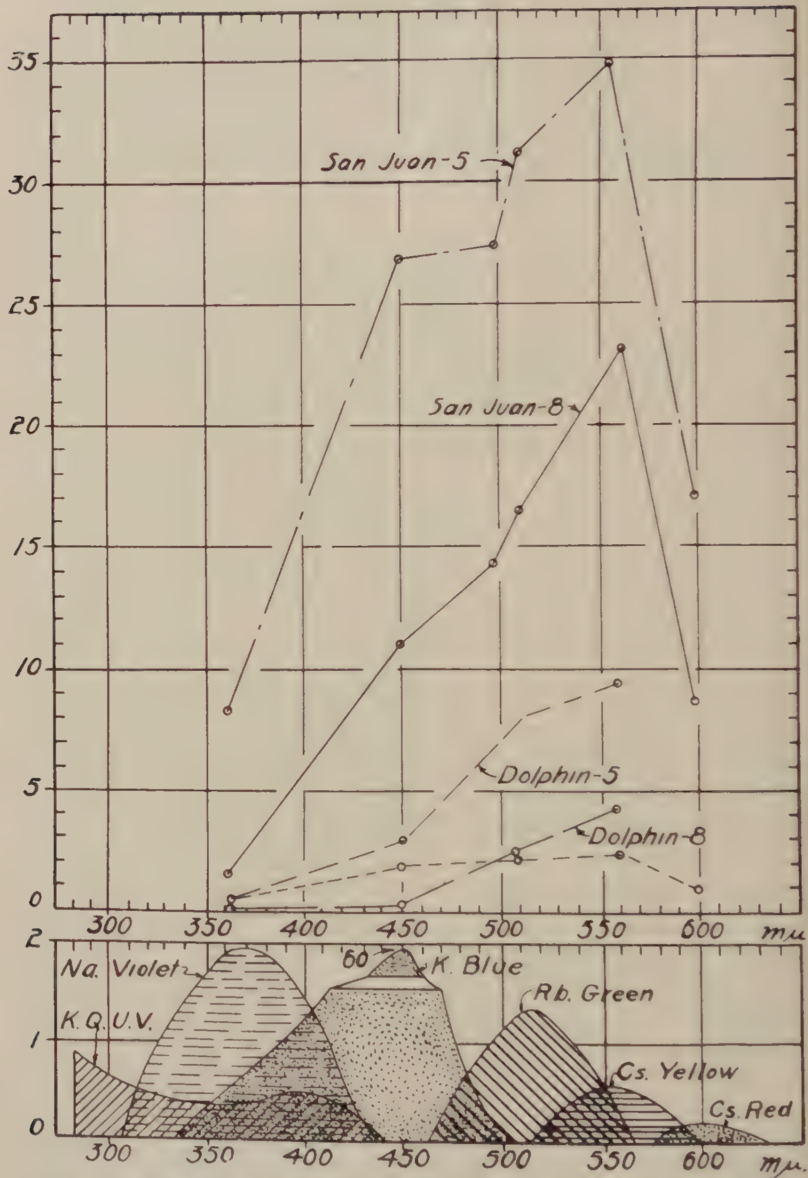


FIG. 192. Showing the difference between the transmission of light by ordinary clear Puget Sound water and by water carrying a dense diatom plankton. The short-dash curve was made by applying the ratio of San Juan 5 meters to Dolphin 5 meters at 360 mμ throughout the series; it indicates that the violet is reduced most.

suspended matter and its characteristics will probably have to be studied in connection with light measurements if these questions are to be settled.

Further comparison of San Juan Channel readings with those made at Dolphin Bay when the plankton was obviously very dense and crowded near the surface, shows that relations of the different portions of the spectrum are maintained but the series shown down to 20 meters in San Juan Channel is essentially crowded together in the first 10 meters (827). This suggests that the plankton and suspended matter are responsible for the effects on the different portions of the spectrum.

The distribution of energy under water may be calculated from such sources as are shown in figure 133 and figure 190*A* when multiplied together. In all cases at moderate depths the maximum energy is in the region of the green and yellow.

IV. MEASUREMENT

1. *Pyrlimnometer* (88, 90)

This instrument, when properly used, measures all the energy of the light entering the water. The type used by Birge and Juday consists of a receiver containing 20 small thermocouples which can be lowered into water to any desired depth down to 10 meters and alternately exposed to the sun and covered. The electrical effect of the sun's radiation on the thermocouples is proportional to the sun's radiation.

It is possible to screen the instrument with heat-absorbing glass and various ray filters, and measure the relative intensity of various portions of the spectrum. The difficulty with this method is that a very sensitive galvanometer is required.

2. *The photo-electric cell*

The construction and operation of this instrument has been discussed (Chapter XIV) so that it remains to be presented only from the standpoint of water. A cell which gives a large current in full light is essential to successful use in deep water or weak light. If the instrument does not come to zero when the cell is darkened, leakage of current is usually the cause, and the trouble we experienced was usually located in the connections between the ends of the twin

cable and the cell terminals, but sometimes above water. A steady boat and clear sky are essential.

a. Cable and insulating material. The cable used in 1920 in Puget Sound Waters was 123 meters (400 feet) of saturated braid

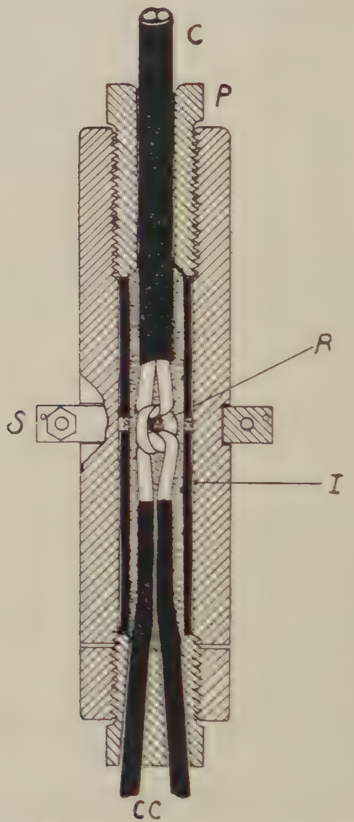


FIG. 193. A, insulator to keep water from entering the covering of the outer cable. *C*, cable; *P*, plug screwed in after the assembly was completed; *S*, supports for wires carrying the basket containing the cell; *R*, short rod for holding the knot in the center of the space; *I*, iron pipe supports for the rod (*R*); *CC*, separated wires covered with gum tubing.

okonite, the so-called brewery cord or packing house cord, which consists of an outer cotton cover thoroughly tarred over a high grade rubber cover surrounding two cotton and rubber covered No. 18 flexible cords. This insulation is supposed to withstand sharp kinking, tying into knots, etc.

The cable used on Lake Mendota was "oko cord," made by the Okonite Company. This consisted of two No. 18 stranded conductors with the usual cloth-covered rubber insulation, imbedded in a rubber covering 10 mm. in diameter. This cable gave about one-seventh as much leakage under high voltage, as the braid covered cord used in the marine work. The leakage compared with minimum current through the photo-electric cells was almost negligible. The weight of the cells and accessories was carried by the cable. To make this possible the two wires of the cable were separated and the outer casing was removed for a distance of four feet. The device shown in figure 193 was used to keep water out of the outer casing. This was also constructed so as to permit the use of wire supports to the cell and accessories. The separate wires were further insulated by greasing them with vaseline and pulling tight-fitting, pure-gum rubber tubing over them.

At Puget Sound a common cell was embedded in a non-conductor. It was first thought that we could embed the cell by filling a prepared box with paraffin. This was done; and when lowered into water leakage occurred after only a few minutes. Various mixtures of Venetian turpentine, bees-wax, sealing-wax and paraffin were then substituted without success. Finally clean vaseline was used; this is sufficiently plastic to push into any vacant spaces and to permit the air to escape. Some of this vaseline was poured over paraffin left in the bottom of the box and on examination after exposure to high pressure it was found that where air bubbles had escaped from the paraffin the vaseline had been pushed into the cavities which they had occupied. In some cases the small cavities were completely filled with vaseline, and in others with a mixture of vaseline and sea water. Vaseline mixed with even very small quantities of harder substances such as paraffin, bees wax, or Venetian turpentine was not sufficiently plastic and water came in contact with the wires. Some of the vaseline after being kept in sea water for three months was tested by inserting the terminals of an 160-volt battery into it with a galvanometer in series. The galvanometer with a sensitivity of 80 megohms showed no deflection when two wires were inserted into this vaseline at a distance of 1 cm. from each other. Similar tests of vaseline which had been used to embed the cell and melted and remelted showed the same result. Vaseline makes an almost perfect insulator.

b. Batteries, reading devices, and cell forms. The battery box, etc.,

described in Chapter XIV was used in study of light penetration into Lake Mendota; and again in Puget Sound in 1926. The instrument used for the reading was a Rawson single pivot ("acrid") microammeter with two ranges of 200 and 20 microamperes respectively. This instrument behaved remarkably well in a small launch 30 feet in length and 1 ton displacement.[2] Even with a strong wind, it offered no serious difficulties in reading, thus exceeding our expectations.

This simple direct-reading equipment is, however, quite inadequate for work below 5 to 10 meters in lakes with large plankton and in turbid rivers. It cannot be used on rough waters. When screens are used it fixes definite limits on the depths to which readings can be made, especially for the longer wave-lengths. A direct-reading galvanometer of some type which will stand the ordinary rocking of a vessel should be in the circuit whenever practicable, but under the conditions where it cannot be read at required depths or for other reasons, a potentiometer equipped with interrupter and head 'phones' should be utilized. The apparatus developed by Poole and Atkins is adequately sensitive and serves as a model for such work.

The form of the cells was changed as compared with the one used in 1920 (830) (fig. 194). The spherical portion was enlarged to 6 cm. in diameter and only the lower half of the surface sensitized. This gave a large surface much more independent of the angle of incidence than was the case of cells used before. The connections with the cable were effected by means of mercury cups (fig. 194). The rubber insulation at the end of the cable wires was removed for about $\frac{1}{8}$-inch and the end dipped into solder. The wire was placed in the mercury in the cup (at first through a cork which later was dispensed with) and covered with melted vaseline. The wire was tied in place to prevent injury to the vaseline insulation.

The cells were fitted into sections of heavy brass tubing with threaded ring tops to hold glass screens in place and solid brass bottoms (fig. 194). Slots were cut in the brass tube to fit the two arms and filling tube of the cell. A large rubber stopper was roughly hollowed out to fit the cell and a quantity of soft rubber (automobile tire

[2] A 10-ton steamboat was used for most of the work on Puget Sound. On these enclosed waters this was fairly satisfactory, but a 10-ton scow towed by a 10-ton gasoline boat, with pilot house control, was steady and generally better, as it was quickly and easily managed. A larger vessel would be needed for work outside of such quiet waters.

putty) placed in the cavity. The cell was then pressed into place and tied down to the brass bottom with strong cord passed through holes in the bottom plate. This gave the cell a perfect fitting bottom on which to rest. The brass plate was wired to the protecting cage (fig. 194) and the large brass tube set over the cell assembly and fastened to the bottom by means of screws. The cells gave from 120 to 220 microamperes in sunlight with 85 volts and 250,000 ohms in series. This voltage and resistance were usually used; 100 and 120 volts were used only between 10 and 15 meters in Lake Mendota

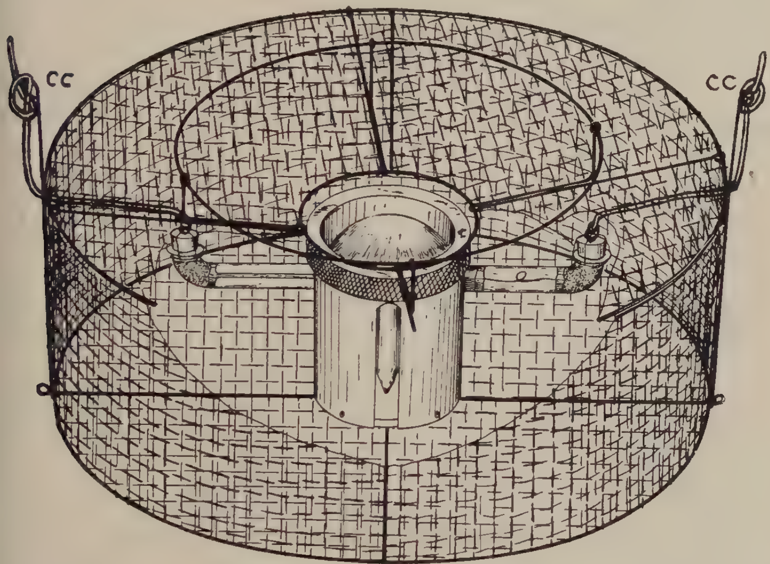


Fig. 194. A cell in position in the protecting basket, with the brass screen older in position; *cc*, cable strands leading to *cc* of Fig. 193. When necesary a weight could be suspended below the basket from *S* of 193 by wire or ord passing through the loops on the basket. This was not required in ake Mendota.

nd below 25 meters in San Juan Channel in one series with the otassium cell. The current-light-intensity curve for these cells vas essentially a straight line up to about 60 microamperes.

c. Ray filters. When screened with suitable ray filters the cells nay be used to roughly determine the penetration of different ortions of the spectrum into water, with great rapidity. The curve or the cell with any glass is the product of the light transmission urve of the glass and the absolute sensitivity curve of the cell. The

ray filters used by the writer were plates of glass, ground, polished, and fitted to the tops of the brass tubes. While a number of glasses were prepared, only the following were used:

(1) Corning Corex (3 mm. thick) over a K quartz cell has its maximum near the limit of the sun's ultraviolet.

(2) Corning Ultra (3 mm. thick) over a Na cell has its maximum at 375 mμ.

(3) Blue D (1.5 mm. thick), which greatly reduces the long wave lengths leaving blue predominating, was used to reduce the sensitivity of the potassium cells to colors other than blue.

(4) Noviol C (Corning) (1.5 to 5.0 mm. thick) was used to restrict the rubidium cell to green and yellow light (Chapter XIV).

(5) Noviol A (Corning) (1.5 mm. thick) was used to reduce or eliminate the violet and near ultra violet.

(6) Corning high transmission yellow (G 30B) (3.2 mm. thick) was used to restrict the caesium cell to yellow and orange.

(7) Corning G 24 (a red pot glass used in railroad signal lights) was used to restrict the caesium cell to orange (Chapter XIV).

The only difficulties encountered were in connection with the use of the glass ray filters. When the cells were lowered, bubbles of air remained below the glass, making it necessary to tip the baskets to a sharp angle. This forced the mercury against the vaseline and caused leaks in two cases. This difficulty was remedied by properly grinding places in the edges of the glass so as to allow the air to escape without admitting light.

The leaks were remedied by renewing the vaseline with some melted over an alcohol lamp on the deck of the launch. One cell was removed and replaced by another under the same conditions.

3. *Other methods*

Various methods noted as provisional in Chapter XIV must often be employed in water as electrometric methods are applicable only in relatively shallow water.

The study of light penetration into water has usually been conducted with Secchi's disc, or with sensitized plates and paper.

a. Secchi's disc. This is a white disc 20 cm. in diameter. It is lowered and the depth at which it disappears and reappears again are noted. The mean between them is used as an index of light penetration (621).

b. Photo-chemical methods. Various methods of exposing photo-
graphic plates and paper have been used. Regnard used a sensitized
paper on a drum turned before a slit by clock work (fig. 191, B). The
Michael Sars (610) carried a Helland-Hensen photometer. This
apparatus consisted of a frame with two side bars on which a plate
holder and cover might slide when released. The plate holder was
nearly cubical, slightly smaller at the top and carried plates on four
sides and at the top. The cover was a box of similar form which
fitted tightly over the plate holder. The plate holder and cover
were latched in place at the top of the frame at the time the instru-
ment was lowered. The first messenger released the plate holder,
which dropped to the bottom of the frame, exposing the plates.
The second messenger dropped the cover to the bottom, covering the
plates and ending the exposure. Light penetration was demonstrated
with this apparatus down to 1000 meters. On June 6 at 31°15′
North Latitude in the Atlantic Ocean the plates showed distinct
light effects after an exposure of two hours at 1000 meters. When
lowered to 1700 meters and exposed for two hours no changes were
noticeable in the plates. The observers came to the conclusion that
light penetrates to a depth somewhere between 1000 and 1700 meters.
This photometer is one of the latest and best types of instruments
for the use of sensitized plates or papers.

Grein found light at 1500 meters and concluded that violet pene-
trated farthest. The writer found Puget Sound water more trans-
parent to violet than to blue or green below about 18 meters (Fig.
190, C).

c. Knudsen spectrophotometers. Knudsen (483) used two spectro-
photometers, one at the top and one at the bottom of the layers of
water to be measured. Ingeniously arranged slits enabled him to
make comparisons of the same wave length at the top and bottom of
the layer to be examined through the effect on the photographic
plate.

d. Klugh's apparatus. Klugh (480, 481) used a series of screens
over photographic plates. This method is inferior to the use of
prisms.

e. The neutral wedge or colored wedge. This principle has been
extensively used in all sorts of measurements of light. Klugh has
also made use of it (480). The distance toward the thick end of the
wedge showing the effects of light on the paper or plate used, is the

measure of the light intensity. Hollow wedges which may be filled with solutions transmitting certain rays have been used to measure certain wave lengths. This method has been used frequently in Europe. A mechanical device in the nature of a shutter which gives a wedge exposure to the plate or paper is most desirable.

f. Selenium. At least one attempt has been made to use the selenium cell. Regnard (719) in 1889 made a series of determinations of light penetrations in the harbor at Monaco using a selenium cell. The galvanometer on which the readings were made was located in the laboratory of the Prince of Monaco, and the cell was lowered into the harbor by means of a long cable. He states none of the difficulties nor precautions connected with the work. His results do not appear consistent with present knowledge.

V. RECORDING AND CONTROL

Continuous recording of light in water at depths of 5 meters or less offers no serious practical difficulties and may be carried out as described on page 345 (Chapter XIV). Control of light conditions is not essentially different from those methods suggested for non-aquatic conditions.

CHAPTER XIX

Chemical Conditions in Water[1]

I. INTRODUCTION

The various responses of aquatic animals determine what chemical factors should be measured. In this case as in others the question as to what conditions are important has never been fully answered. Marsh's statement (574), that freshwater fishes of the same species live and thrive in water with from 20 to 480 parts per million of dissolved salts, tallies with the facts brought out in the preceding chapter relative to osmotic pressure relations in this group. It is also well established that freshwater fishes will live in distilled water if it is free from poisonous metals, commonly added in distilling. These findings tend to throw the rôle of dissolved salts in fresh water into a field of secondary significance. Unfortunately, very little is known of the relations of groups other than the lower vertebrates and protozoa.

The salts of sea water are either essential or of great importance to marine animals. The fact that *Fundulus* will live in distilled water but is killed by NaCl of sea-water concentration unless small amounts of calcium and potassium chloride are added, and similar phenomena led Loeb to the theory that the calcium and potassium salts are necessary to neutralize the toxic effects of the NaCl. Loeb further showed that carbonates or bicarbonates are necessary to the neutralization of the acid formed by the body and to the production of skeletons. A very large literature has been produced in this field which is well summarized by Loeb (530), Wells (963) and Garrey (326) (see also 13, 81, 149, 995).

On the other hand, however, attention has been concentrated on the relations of animals to the dissolved gases involved in the respiratory exchange. First, much attention has been given to the oxygen

[1] The writer is indebted to E. B. Powers for supplying him with information contained in unpublished papers and for assistance relative to carbon dioxide pressure; to S. L. Neave, chemist of the Illinois State Water survey, for criticising the chapter, especially the part on carbon dioxide pressure; to C. Juday for reading and criticizing the chapter; and to W. C. Allee for suggesting several changes in content.

supply in water, the minimum oxygen required by aquatic animals, etc. These investigations have left much to be desired, and the correlation of distribution, growth, and success with oxygen content of water is not striking. Carbondioxide was also determined by the routine chemical titration methods but failed quite completely to show the consistent relations which might have been expected from the important relations of CO_2 in the bodies of higher animals, as well as some of the invertebrates and lower vertebrates of the waters. The amount of weak alkali in the body fluids or surrounding medium obviously influences its actual relationship to the organisms. The determination of hydrogen ion concentrations next occupied the center of attention.

Investigation of hydrogen ion concentration of natural waters by various persons in the past ten years has led to the conclusion that it is an unsatisfactory index of the factors in the environment having effects on organisms. The same conclusion was reached earlier relative to carbon dioxide as determined by titration with alkali and relative to alkalinity as determined by titration with acid and calculated as parts per million of calcium carbonate. The waters examined by the writer and waters modified by him in experiments with fishes were in no case suspected of having organic acid, and in none of the experiments was the amount of acid added such as to break down all the carbonates (pH 4.0). Accordingly, the pH as reported was a function of the dissolved carbon dioxide and the carbonates present. Recently it has become evident that CO_2 pressure is a better index of environmental conditions than pH. If so it is probably due to the fact that CO_2 in simple form exists in water along with H_2CO_3. Several writers largely under the influence of the English physiologists have sought means of determining the CO_2 pressure in the organism as well as in the surrounding medium.

II. CHEMICAL CONDITIONS IN WATER (865)

Salts, salt concentration (167), nitrates (252, 253), oxygen, and carbondioxide demand attention (922, 923, 948). The relation of CO_2 and bicarbonate and other buffers appears to outweigh oxygen content in difficulty of study if not in actual importance. It will, accordingly, be taken up first.

1. Carbondioxide, carbonates, and hydrogen ion concentration

Nearly all natural waters are solutions of carbonates and CO_2, with other salts which modify the relation in a minor way. NaCl (in quantity in sea water) and sulphates and chlorides of magnesium,

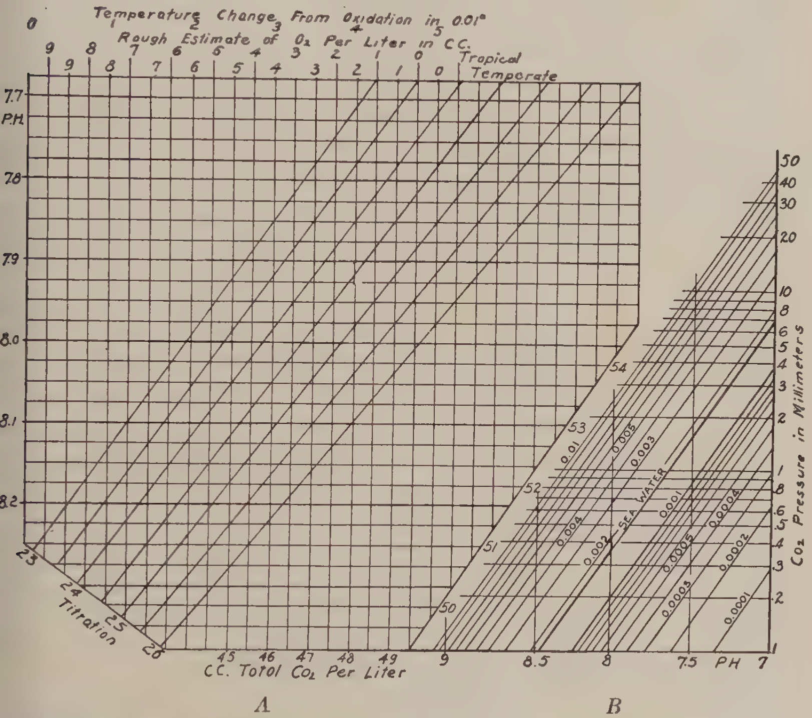


Fig. 195. Showing the relation of various chemical conditions in water. (After McClendon (552)). *A*. Conversion table for finding the total CO_2 of sea water from the pH and alkali reserve (cubic centimeters of 0.1 N HCl to titrate 1 liter of boiling sea water). The total CO_2 is measured on the ordinates and the pH on the abscissae. Each diagonal is for sea water of the alkaline reserve indicated. At the top is given the expected O_2 per liter for tropical and again for temperate oceans. If the change in CO_2 is due to animal oxidations, the temperature change caused thereby is indicated in hundredths of a degree.

B. Conversion table for finding the CO_2 tension at 20° of bicarbonate solutions, and sea water, from the pH. A simple calculation may be made for any other temperature since, if the CO_2 tension is kept constant, the pH varies directly with temperature, 1° corresponding to 0.01 pH. The CO_2 tension in millimeters of mercury is marked on the ordinates and the hydrogen ion concentration is marked on the abscissae. At the bottom is a scale for measuring the pH on the abscissa. The light diagonal lines denote pure bicarbonate solutions, the normality of which is indicated. The heavy diagonal denotes sea water.

calcium, sodium, and potassium usually occur. These salts, other than carbonates, do not modify the CO_2 pressure materially. Phosphates, which may operate in this fashion, occur in such small quantities as to have very little effect.

a. Carbondioxide pressure. The meaning of carbondioxide pressure may be illustrated by the following facts: If a jar connected with a manometer is half filled with water highly charged with carbondioxide (soda water) and quickly closed, the manometer will show a rise of pressure (for the gas in the jar) until an equilibrium is established between the carbondioxide in the air above the water and in solution in the water. Water in contact with air and in which carbondioxide is formed by decomposition and the respiration of organisms is constantly tending toward an equilibrium with the very low CO_2 pressure

TABLE 49

Range of pH in water from natural streams, aerated with air high in CO_2 content

CO_2 PRESSURE	RANGE OF pH
mm. Hg	
0.295	4.50 to 8.50
2.415	4.46 to 7.75
5.331	4.37 to 7.32
11.23	4.18 to 6.96
25.39	4.14 to 6.54
50.68	4.08 to 6.35

of the air, but because of lack of rapid enough circulation and lag in diffusion the carbondioxide pressure of most natural waters is higher than the CO_2 pressure of the atmosphere, which is $.003 \times 760$ mm. Hg or approximately .228 mm. of Hg at sea level (900).

The relations of CO_2 pressure, pH (see page 485 for discussion) and carbonates in a solution of bicarbonate and sea water, which is a little less than 1/500 normal carbonate, are shown in figure 195.

Powers (687, 696, 698) has shown that in water from natural streams, aerated with air high in CO_2 content, the pH may range as shown in table 49.

Saunders shows that pressures of 0.228 mm. to 7.30 mm. in Cambridge (England) tap water are accompanied by pH 8.86 to 7.20 while the HCO_3 is 0.0044 normal.

These data indicate that pH alone tells little or nothing relative

to CO_2 pressure, which is probably the effective factor so far as organisms are concerned.

Other methods of measuring CO_2 are inadequate. Titration with alkali as commonly practiced in water analysis is not a measure of CO_2 pressure. In the waters examined by Powers, water with approximately pH 8.0 varied from approximately 0.3 to 1.2 mm. of CO_2 pressure, in correlation with the alkaline reserve. Saunders indicates the relations shown in table 50.

It appears from Saunders' (775) data that the CO_2 pressure increases with increase in alkalinity at the same hydrogen ion concentration.

b. Alkalinity or buffer value. Determinations of "alkalinity" have long been among the means used for ascertaining the suitability of a

TABLE 50

Showing the relation of HCO_3 and alkalinity (calculated as Na instead of $CaCO_3$) to CO_2 pressure at pH 8.0, etc. (from data by Saunders (775))

SOURCE OF WATER	HCO_3 NORMALITY	Na NORMALITY	pH	CO_2 PRESSURE
				mm. Hg
Cambridge tap and distilled	0.0023	0.0023	8.16	0.72
Cambridge tap	0.0044	0.0050	8.16	1.24
	0.0044	0.0050	8.00	1.61
Calcite in distilled water	0.0027	0.0027	7.99	1.295
Sodium bicarbonate and NaCl	0.00093	0.6000	7.96	0.228
Sea water I	0.0026	0.60	8.36	0.228
Sea water II	0.0024	0.60	8.35	0.228

water for domestic and industrial purposes. The relations of this property of a water to organisms had never been fully appreciated until recently when its value as an expression of the capacity of a water to neutralize CO_2 was recognized.

There is great confusion as to methods of measuring and expressing "alkalinity." It is expressed (a) in terms of a carbonate of a predominating alkaline metal—for example, as $CaCO_3$; (b) as bound and half-bound CO_2; (c) as alkali reserve; and (d) as buffer value. It is from time to time confused with total CO_2 and the normal acid used in titration.

The alkalinity or buffer value of a water in routine water analysis is ordinarily determined by titration with standard acid to about pH

4.0 or 4.2 (turning point of methyl orange) at which point the carbonates are all broken down. Alkalinity is commonly calculated as calcium carbonate because in many localities this is the chief alkali in surface waters. To avoid this uncertainty as to alkalies present, some biologists have merely given the amount of normal acid used. It is best to calculate alkalinity as parts per million or normality of CO_3, and bicarbonates as parts per million or normality of HCO_3.

TABLE 51

The pH scale and relative amounts of free hydrogen ions

pH	Relative concentration of hydrogen ions	
0	10,000,000	("Normal" H ions)
1	1,000,000	Acid
2	100,000	
3	10,000	
4	1,000	
5	100	
6	10	
7	1	Neutral
8	0.1	Alkaline
9	0.01	
10	0.001	
11	0.0001	
12	0.00001	
13	0.000001	
14	0.0000001	("Normal" OH ions)

This leaves the cation to be anything that it may. The fact that calcium or any other common alkali metal behaves thus:

$$CaCO_3 + H_2CO_3 = Ca(HCO_3)_2$$

is the basis for the neutralization of CO_2 produced by organisms. Usually, however, both $CaCO_3$ and $Ca(HCO_3)_2$ exist in solutions and the fact that $CaCO_3 + 2HCl = H_2CO_3 + CaCl_2$ or $Ca(HCO_3)_2 + 2HCl = CaCl_2 + 2H_2CO_3$ while the H_2CO_3 breaks into H_2O and CO_2 the latter escaping into the air, shows how carbonates neutralize strong acids. It is this process by which carbonate free water is produced (see p. 502). The process of determining buffer value is essentially the same in water analysis and physiology, namely titration with acid to pH 4.0 or 4.2. If the water is pH 8.0 the carbonates

are all present as bicarbonates and the amount of CO_2 in the bicarbonate is double that which would occur if the solution was carbonate.

c. Hydrogen ion concentration (44–47, 463). Generally speaking, the determination of hydrogen ion concentration and carbondioxide pressure are among the most complicated problems confronting students of fresh-water ecology. As will be shown later, the determination of H ion concentration is an essential step in determining carbondioxide pressure in the field.

Hydrogen ion concentration expressed as pH is the logarithm of the reciprocal of the normality of free hydrogen ions. The pH scale and relative amounts of free hydrogen ions are as shown in table 51.

The range to be expected in fresh waters is about 8.5 to 6.5 for most uncontaminated streams and lakes. Streams receiving mine seepage may have much higher hydrogen ion concentrations and still support certain species of fish. (144, 166, 190, 463.) The sea is usually about 8.2 (590).

Although hydrogen ion measurements (213, 673) in natural waters to date usually lack continuity, they show some correlations with biological phenomena. It is not surprising that pH readings taken at more or less irregular intervals or for short periods have failed to correlate with distribution and activity in animals especially since it is a poor index of CO_2 pressure. Table 52 shows some typical conditions of pH. Important relations of CO_2 pressure, alkalinity and pH are shown in table 53 as well as suggestions as to variations in the same stream, (compare Ferndale and Mount Vernon and Hood River with Portland in 1920 and 1923).

Figure 196, prepared by Dr. R. E. Greenfield (351), shows the chemical relations of $CaCO_3$ (alkalinity) and free CO_2 (titration method) as expressed in a former paper (Greenfield and Baker). A ruler placed on the alkalinity and free CO_2 crosses the pH scale at the approximate pH of the water. Thus, since all the salts are not ordinarily in the form of carbonate, a water with total solids of 40 parts per million and 6 parts per million of CO_2 would nearly always be acid. The formula does not hold for the polluted Illinois River, some well water, etc.

d. Relations of pH to putrescibility and pollution. Under ordinary conditions putrescibility accompanies high free CO_2. This is determined partly, however, by alkalinity, but with a constant alkalinity, CO_2 usually varies directly with the putrescibility. In the Illinois

River, with an alkalinity of 100 to 140 parts per million of $CaCO_3$, samples show pH values up to 7.2 with CO_2 at 8 parts per million several days after being shipped from points above Chillicothe. Here the calculated values of Greenfield and Baker were about 3 points too high, which was probably because the formula gives incor-

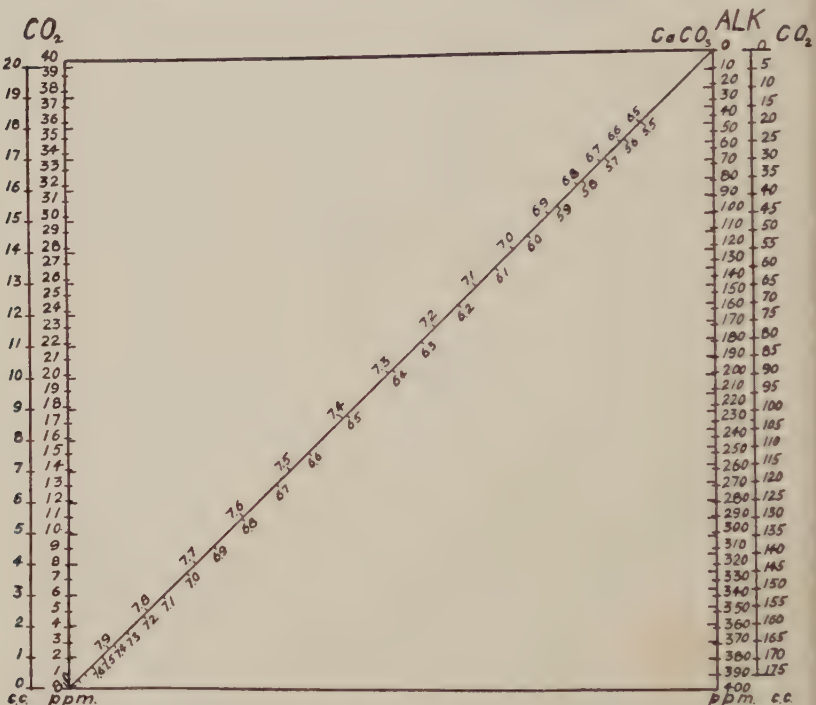


FIG. 196. A chart prepared by Dr. R. E. Greenfield (351) for determining the third condition of a water when two of three, viz.: free carbon dioxide, "alkalinity," i.e., $CaCO_3$, and hydrogen ion concentration, are known. Both right and left scales must be read on the side of the square. The pH figures at the left and above the diagonal are for use with the right-hand scale as it is, while those below and to the right are for use with one tenth of the right-hand scale. A straight-edge passing through two known conditions of a water crosses the other at approximately the third condition.

rect results in the presence of free ammonia. The low CO_2 values are surprising for the Illinois River. Farther down the stream, at Chillicothe, Ill., September 6, 1919, the pH was 6.8 at the surface, and 6.9 at the bottom with green algae in evidence, and 0.9 cc. O_2 per liter at

TABLE 52

Colorimetric estimation of the hydrogen ion concentration of waters belonging to the Puget Sound and Columbia River drainage basins, in 1920 (822)

The samples are from near the surface except the second items for some localities which are from one meter depth when not indicated. The dates are for August, the day of the month being given under "day." Letters used have the following meaning: *R* = swift; *M* = moderate current; *Q* = still water; *S* = shallow; *T* = turbid; *C* = clear; *V* = rooted vegetation; *a* = algae.

STREAM	LOCALITY	STATE	pH	TEMPERATURE °C.	DAY	HOUR	A. = A.M., P. = P.M.	REMARKS
Fraser River*	Steveston	British Columbia	6.9	18.0	7	10	A.	*MT*
Fraser River	Vancouver	British Columbia	7.0	18.0	7	12	M.	*MT*
			6.9					
Nooksack River	Ferndale	Washington	6.5	17.5	8	9	A.	*MT*
Jc. Sqalmic Creek	Bellingham	Washington	7.0	20.0	8	11	A.	*MCa*
Jc. Sea near Sqalmic Creek	Bellingham	Washington	8.1	12.0	8	11	A.	*QCa*
½ Sea ½ Creek	Bellingham	Washington	7.7	20.0	8	11	A.	—
Skagit River	Mount Vernon	Washington	6.7	17.0	25†	8	A.	*MT*
Columbia River	Vancouver	Washington	7.1	16.0	9	11	A.	*MT*
			6.5					
Jc. Columbia River	Hood River	Oregon	7.2	16.0	10	9	A.	*MC*
			7.0‡					
Jc. Hood River	Hood River§	Oregon	6.9	15.0	10	8	A.	*RT*
Columbia River	Arlington	Oregon	7.3	16.0	10			
			7.2‖					
Jc. Grande Rapids River	Hilgard	Oregon	8.1	24.5	13	12	M.	*RC*
Jc. Five Points Creek	Hilgard	Oregon	6.7	23.0	13	12	M.	*RC*
Five Points Creek	Hilgard	Oregon	8.5	23.0	13	12	M.	*QCa*
Jc. Grande Rapids River	La Grande	Oregon	8.5	28.0	11	12	M.	*QVa*
Jc. Catherine Creek	La Grande	Oregon	8.4	27.0	11	12	M.	*QVa*
			7.4					
Willow Creek	Summerville	Oregon	6.9	20.0	12	5	P.	*M*
Grand Rapids River	Elgin¶	Oregon	7.9	28.0	12	4	P.	*MT*
Jc. Minam River	Minam	Oregon	6.7	22.0	11	5	P.	*RC*
Jc. Wallawa River	Minam	Oregon	8.4	24.0	11	5	P.	*RC*
Jc. Minam River	Minam	Oregon	6.6	23.0	12	3	P.	*RC*
Jc. Wallawa River	Minam	Oregon	8.4	24.0	12	3	P.	*RC*
Wallawa River	Enterprise	Oregon	7.4	11.0	12	7	A.	*RCa*
Wallawa L outlet	Joseph	Oregon	7.1	20.0	12	8	A.	*CM*
Wallawa L head	Joseph	Oregon	7.0	20.0	12	9	A.	*CM*
Wallawa L inlet	Joseph	Oregon	6.9	11.0	12	10	A.	*CM*
West Fork Wallawa River	Joseph	Oregon	6.5	11.0	12	11	A.	*RC*
East Fork Wallawa River	Joseph	Oregon	6.7	11.0	12	11	A.	*RC*
Jc. Snake River	Bliss	Idaho	8.1	19.5	14	4	P.	*MC*
Jc. Malad River	Bliss	Idaho	8.0	17.5	14	4	P.	*RC*
Portneuf River	Pocatello	Idaho	8.1	20.0	17	10	A.	*MT*

* August, 1921, Cameron and Mounce found 7.6–7.8, with high alkalinity. The difference is easily within the range of variation in alkalinity; see Johnson, 1921.

† 1922.

‡ 0.5 meters deep.

§ Roadside pool at Dalles QVa 7.6, 29°.

‖ 2.5 meters deep.

¶ Waters had been used for irrigation.

TABLE 53

Giving data as indicated in the respective headings of the columns of the table of the natural waters of the western portion of the United States in 1923

Column 6 is an acid methyl orange titration.

The data in each column are recorded in the same order as given in the heading of the column; CO_2 pressure in column 3 is after aeration. (From data by Powers, 694.)

(1) Stream and location	(2) Temperature of water and air, date in 1923	(3) RpH and CO_2 pressure in mm. Hg	(4) pH and CO_2 pressure of rivers draining lakes, oxygen in cc. per l.	(5) pH and CO_2 pressure of rivers not draining lakes, oxygen in cc. per l.	(6) Alkalinity as $N/10,000$ alkali
Fraser River, near Hammond, B. C.	17.5° 22.0° 8/10	7.75 0.21	7.58 0.41 6.65		5.47
Nooksack River, Ferndale, Wash.	16 0 14.5° 8/10	7 60 0.22		7.12 1.14 6.71	4 05
Skagit River, Mount Vernon, Wash.	14.5° 28.5° 6/11	7.98 0.21	7.75 0.35 6.89		3.11
Stillaquamish River, Pacific Highway, Wash.	20.0° 26 0° 8/11	7.89 0.21		7.15 1.29 6.25	4.88
Cedar River, Penton, Wash.	14.3° 21.0° 8/13	7.72 0.21		7.37 0.52 7.30	4.16
Nisqually River, near Tacoma, Wash.	15 5° 21.0° 8/14	7 72 0.21		7.13 0.95 6.97	3.63
Cowltz River, near Oregon City, Ore.	20 0° 19.5° 8/14	7 60 0.21		7.15 0.80 6.38	3.95
Columbia River, 31 miles above Portland, Ore.	20.3° 20.5° 8/15	8.28 0.21	8.21 0.25 7.10		8.66

TABLE 53—*Continued*

(1) STREAM AND LOCATION	(2) TEMPERATURE OF WATER AND AIR, DATE IN 1923	(3) RpH AND CO_2 PRESSURE IN MM. Hg	(4) pH AND CO_2 PRESSURE OF RIVERS DRAINING LAKES, OXYGEN IN CC. PER L.	(5) pH AND CO_2 PRESSURE OF RIVERS NOT DRAINING LAKES, OXYGEN IN CC. PER L.	(6) ALKALINITY AS $N/10,000$ ALKALI
Sandy River, 25 miles above Portland, Columbia River	19.0° 20.5° 8/15	7.71 0.21		6.82 1.37 6.70	3 33
Willamette River, Milwaukee, Ore.	18.0° 27.5° 8/15	7.87 0.21		7.37 0.72 7.00	4 33
Santiac River (Ore.), near Willamette River	22.0° 29.0° 8/15			7.20 4.07	3.29
Willamette River, Albany, Ore.	22.5° 22.5° 8/15	7.86 0.20		7.18 1.78 6.55	4.07
Umpqua, North Fork, Roseburg, Ore.	20.3° 28.0° 8/16	7.87 0.20	7.41 0.64 6.32		4.21
Umpqua, South Fork, near Roseburg, Ore.	24.5° 31.5° 8/16	8.27 0.20		7.85 0.53 6 28	6.17 5 85
Rogue River, Grant's Pass Park, Ore.	20.5° 26.0°	7.88 0.19	7.82 0.22		

the bottom, 20 feet from the west shore. On September 3, at Liverpool more than 50 miles farther down stream we found pH 6.9 at the bottom and 0.96 cc. O_2 per liter, with the bottom fauna destroyed. The fact that CO_2 values appear to be small in this stream makes the calculated pH values too high. Calculated values should not be used except where determinations are not practicable, e.g., in working over old data. Too many waters contain ammonia or other disturbing substances.

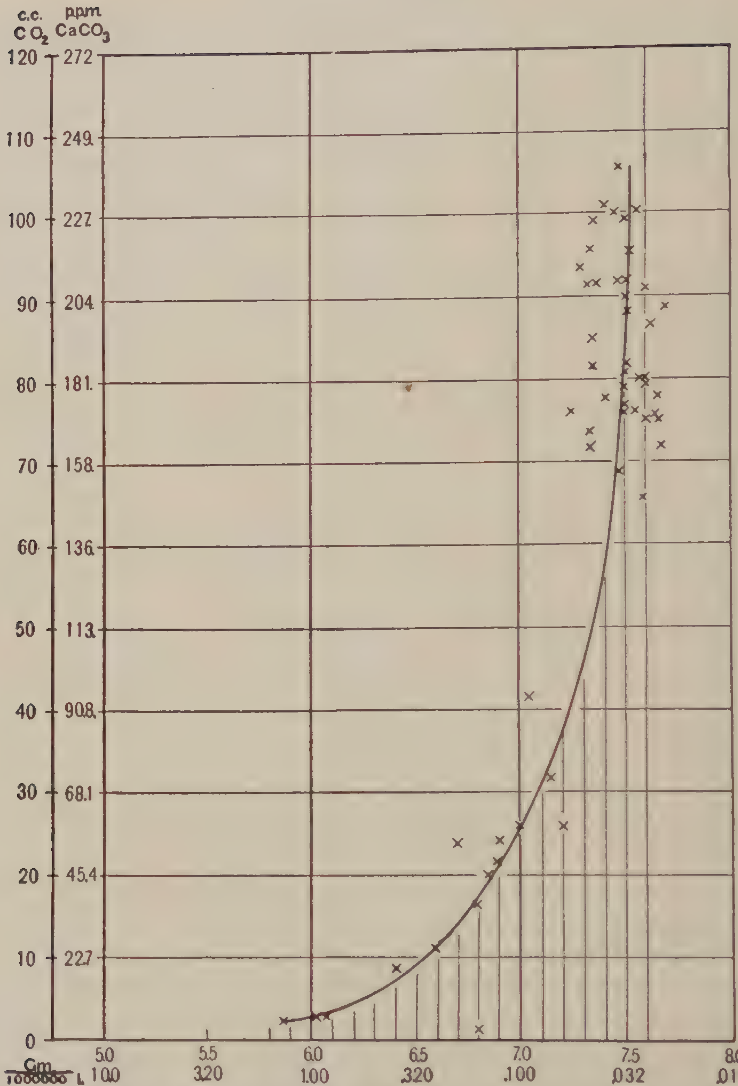


FIG. 197. Showing the range of hydrogen ion concentration accompanying a trace of oxygen in Wisconsin lakes. Calculated from data obtained by Birge and Juday (89). At the left, alkalinity is shown as CO_2 and $CaCO_3$; below, hydrogen ions, as pH and as grams per million liters.

2. *Dissolved oxygen and hydrogen ion concentration*

Dissolved oxygen, which is nearly always present in natural waters, usually is correlated with CO_2 content, especially if the "alkalinity" is fairly constant. A fairly constant alkalinity exists in the sea. McClendon (552) states that "in so far as the sea is a closed system; O_2 varies inversely with CO_2, due to the action of organisms, the possible error being 30 per cent." He presents a chart (see fig. 195) showing the amount of oxygen to be expected in sea water of various "alkalinities," etc. Below the thermocline, a lake in summer is a closed system, and in so far as alkalinity remains constant there is an inverse relation of O_2 and CO_2, which is, however, by no means constant. Figure 197 shows this relation. This stability of the O_2 and CO_2 values probably depends upon uniformity of circulation, diffusion, changes in alkalinity, etc., but *in all the work described herein* there is an inverse relation between pH and O_2. When hydrogen ion concentration is decreased (due to reduced CO_2 pressure indicated by higher pH figures) dissolved oxygen is increased.

3. *Salt content and age*

The salt content of a water is determined by its "age," i.e., the time since it melted from snow or ice or fell as rain, and by the kind of materials over which it flows. Igneous rock frequently gives a small salt content, but its chemical composition is more important than the fact of being igneous.

As the altitude increases in a mountainous country the hydrogen ions usually increase and salt content decreases. That is, buffer is low and CO_2 is not neutralized.

4. *Tropical rivers*

The Amazon River with 37 to 59 parts per million solids, of which Ca, Mg, Na, and K comprise 25.09 to 27.94 per cent, and CO_3 24.15 to 34.75 per cent of the total, suggests acid waters. The immense plant growth in its basin supports this idea. Allee and Torvik (21) found the pH of a small stream in the tropical rain forest of Panama in the dry season to range from 6.1 to 6.9 in the upper pools while the lower pools near Gatun Lake showed pH 7.2 to 7.9.

The total solids of four out of six rivers of British Guiana amount to 45 parts per million or less. In South America the total solids

increase as we go south to more arid parts. Rivers of India and Java show higher salt content though the rainfall is great. These seem not to follow the usual rule. The amount of carbonate suggests relatively low hydrogen ion concentration.

5. Stream junctions

Where two streams meet, differences in conditions are due to age of waters, etc. With two waters of unequal age, four or more differences occur: In hydrogen ions, in temperature, and in quality and quantity of dissolved content (see table 54).

As between the Columbia and Snake, the Chinook salmon chooses the Snake. The stream junctions visited by the writer are indicated in table 52 by brackets and by the abbreviation "Jc." In practically all cases there is a marked difference in H ion concentration as well as in temperature. The case of the Wallawa and Minam is striking (table 52). The temperature difference between the two streams is 1 to 2° and the pH difference 1.8. Powers also noted a difference 4.2°C., of 0.44 in pH, and 2.5 N/10,000 alkalinity between two forks of the Umpqua (Or.) (table 53).

TABLE 54

Conditions at stream junctions; figures are parts per million

	TOTAL SOLIDS	CO_2	HCO_3	Ca	Mg	Na-K
Columbia.........	83	25.9	73.0	18.0	4.5	6.0
Snake.............	131	55.4	83.0	19.0	5.6	1.4

6. Conditions in soils

Soil animals during heavy rains and in submerged soils are essentially in water as all air is driven out of the soil. Conditions surrounding them are the same as aquatic animals. The water which forces the air out is saturated with air (oxygen) when it enters. We know of no determination of the O_2 content of soil water. For this purpose water from lysometers (see pp. 129 and 130) should be used.

III. EFFECT OF CHEMICAL CONDITIONS ON ORGANISMS (184, 553)

There is very little known as to the effect of CO_2 pressure upon organisms. The chief experiments along this line have really con-

sisted in varying the amount of carbonate, adding some other salts, and varying the amount of CO_2. This is due to the fact that most waters contain sufficient carbonate to neutralize all the acid ordinarily added, resulting in liberation of CO_2. Unless the resulting pH falls below 5.6, no free acid is to be expected in ordinary waters originally of pH 6.5 to 8.0. Experiments have been concerned as a rule with the variation of CO_2. Jacobs called attention to the difference in effects of CO_2 and other acids and found as Powers had suggested that it penetrated organisms much more readily. There have been very few studies of CO_2 pressure in water in relation to its effects upon aquatic animals. Hyman (426) has demonstrated that it is CO_2 and not hydrogen ions which has important effect upon the growth of planaria. She believes that it is CO_2 generally. A study (1911) of the reactions and resistance of fishes appeared to indicate that CO_2 was of great importance (828, 829).

1. *Higher vertebrates* (282, 321)

Mammals, birds, and reptiles are not ordinarily in contact with water in such a way as to be affected by hydrogen ion concentration. It was the fact that the former group maintains close regulation which lead to the belief in the importance of hydrogen ions, in particular the injection of acid into the blood stream led to the conclusion that all acids act alike. Mammals appeared to give the result similar to increased CO_2 but mineral acid would at the same time have the effect of increasing the carbondioxide by liberating it (60, 61, 164) from the buffer of the blood (398, 401). The close regulation of the blood, alveolar air, various secretion processes (264) in the mammals led to the belief that hydrogen ion concentration is of great importance to animal life. This is however so largely the hydrogen ion concentration of the H_2CO_3, that pH is a good index.

The pH of the blood serum when CO_2 content is brought into equilibrium with air by atomizing, was called RpH by Marriot (572, 573) and is a very exact index of the buffer or alkaline reserve of the blood (231, 293, 918–921).

The CO_2 pressure of alveolar air is very constant and small changes in it produce marked effects in mammals. This is evidenced by mountain sickness, which has led to the conclusion that CO_2 pressure is of much importance. It is probably a true measure of CO_2 as acting within the organisms. Various methods of determining gas

pressure in blood and fluids have been devised. Some of these consist in introducing a bubble of N_2 or mixture of atmospheric gases into the fluid. One of the bubble methods for physiological fluids is described and the results checked against those of the Barcroft tonometer by Poulton and others (684). Krogh was also an early contributor to this field. The CO_2 pressure studies of these Danish and English physiologists show something of the importance of this subject.

2. Fishes

Fishes have proven a favorite material for experimentation.[2]

a. Reactions. Fishes react to hydrogen ion concentrations. A large series of experiments was conducted by the author in 1923 with ten species of fish and a number of types of water: aerated deep-well water, boiled water, distilled water, rain-water, etc. In nearly all cases the fishes reacted definitely to differences. With any given temperature, salt content, etc., they usually behaved consistently, and with any one set of conditions could be depended on to select a given hydrogen ion concentration; but as conditions were varied and the number of readings increased the results varied, indicating that actual control lay with another factor. The selections tend to fall in two or three places, which with a larger number of readings would probably be reduced to one maximum. Each species appears to have a definite range which differs from every other species. Na_2CO_3 shifts the selection to lower hydrogen ion content. An average of approximately twelve experiments were run with each species. The range selected by each species is rather wide, though with a few exceptions the fishes show unmistakable evidences of reacting to gradients of hydrogen ions. Fishes accustomed to live in clear open waters, especially the minnows, select the lower hydrogen ion concentrations. It is evident from the range of concentrations selected by them that

[2] The writer is indirectly responsible for erroneous statements by Wells (964). He referred to neutrality and it developed later that he had called pH 8.0, the turning point of phenolphthalein in water analysis, 'neutral' and made statements as to the optimum acid concentration for certain fishes, whereas his experiments were run in distilled water containing carbonates and were therefore nullified. In 1923 (821) the writer published the results of repeating a part of Well's experiments. Meanwhile erroneous statements as to neutrality and alkali relations were introduced into 943 and copied in Shull's text on zoology.

all these species might be found in the same small stream during non-critical periods. The order in which the species arrange themselves corresponds to the frequency of their occurrence in natural bodies of water. (905.)

TABLE 55

Showing the effect of hydrogen ion concentration on the survival of rock bass in low-oxygen water, August, 1918

NUMBER OF FISH	WEIGHT	SURVIVAL	pH	O_2 PER LITER	TEMPERATURE
	grams	*minutes*		*cc.*	*°C.*
a	10.0	43	6.0	0.42	16
b	10.0	55	6.5	0.22	16
c	11.5	50	6.2	0.68	16
d	14.5	1500+	6.5	0.79	16
e	16.0	71	6.1	0.70	16
f	18.0	350	6.5	0.79	16
g	18.0	60	6.2	0.68	16
h	21.0	55	6.5	0.42	16
i	28.0	45	6.3	0.28	16
j	138.0	124	6.0	0.72	16

TABLE 56

Showing the effect of hydrogen ion concentration on the survival of large-mouthed black bass in low-oxygen water, January, 1921 (821)

	NUMBER OF FISH	AVERAGE WEIGHT	SURVIVAL	pH	O_2	TEMPERATURE
		grams	*minutes*		*cc.*	*°C.*
a	6	346	84	8.6	0.18	13.5
	6	287	62	6.5	0.18	13.5
b	7	275	64	8.5	0.055	13.5
	6	285	47	6.2	0.06	13.5
c	2	255	70	8.5	0.06	13.5
	12	328	63	7.6	0.06	13.5
	10	320	50	6.2	0.06	13.5

Powers (688) found definite selections on the part of herring and various young salmon both in experiments and in nature. His herring in the vicinity of Friday Harbor, Puget Sound, selected pH 7.7, while herring were more abundant near Namino, British Columbia, in water lower in hydrogen ions.

Jewell (441, 443) Brown and Jewell (119) made studies of one very acid lake (pH 4.4) which contained fish, and found that fishes from adjacent lakes with very different hydrogen ion concentration selected the kind of water from which they were taken, a fact which suggests acclimation. Reactions to oxygen content are much less definite than to hydrogen ions (CO_2). A certain amount of regulation is accomplished by the swimbladder (366).

b. Survival. The survival experiments of Jewell appear to be particularly significant as she found that fishes from a very acid lake and from an alkaline lake survived when transplanted. Certain

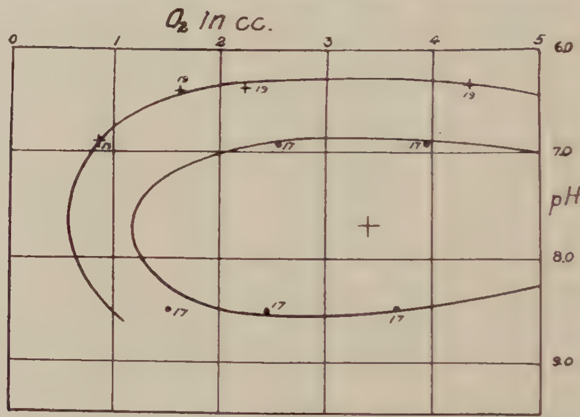


FIG. 198. Showing equal time lines on an oxygen-hydrogen-ion chart (364). The solid lines pass through combinations of oxygen and hydrogen-ion concentration in which the embryos developed short fin rays in seventeen and nineteen days, respectively. The general trend of these lines suggests that development may be expected to be most rapid at about 3.4 cc. of oxygen and pH 7.6 to 7.7, where the large cross is placed. The cross is in the center of the ellipse.

acids such as *tannic* and *humic* appear to be quite harmless. It is further evident that some measure of the CO_2 concentration as effectively acting on the aquatic animal is an essential thing to determine. There was abundant oxygen in both lakes.

Survival experiments have shown that there is an important relation between hydrogen ion concentration (CO_2) and survival in low oxygen. CO_2 was liberated from carbonates by adding acid, but no free H_2SO_4 or HCl occurred though the alkaline reserve was reduced.

Comparing individuals *a*, *b*, and *c* (table 55) it is evident that a change of 0.5 on the pH scale is more important than one of 0.20 cc.

in O_2 and that a decrease of 0.3 on the pH scale equals in effects a difference of 0.46 cc. in oxygen. Furthermore, fish *c* was heavier than *a* or *b*, and the larger fish usually live longest. Fishes *f* and *g* show a striking difference in survivial when both pH and O_2 are moved in the unfavorable direction. Fishes *h* and *i* are similar to *f* and *g*, but the 28-gram fish (*i*) should have lived longer considering its larger size.

The survival of fishes under conditions of natural waters has never been studied experimentally. The limits as to oxygen, CO_2, etc., could be worked out in connection with hatcheries and culture ponds, provided that some of the experimental devices described herein were installed where treated water could be brought into contact with fishes under conditions in which they can live normally.

c. *Fertilization.* Hall (364) found that when oxygen is 4 cc. per liter fertilization of the eggs of the whitefish takes place equally well in acid, neutral, and alkaline waters. When oxygen is lower (2.9 cc. per liter) pH 6.2 to 6.6 is more favorable to fertilization[3] than 7.0 to 8.4. Clowes and Smith (185) found neutrality especially detrimental. This relation is quite inexplicably the reverse of what would be expected by comparison with other relations to oxygen.

d. *Development.* Hall (364) worked on white fish eggs and found the rate of development in relation to O_2 and pH (CO_2) rather complicated. Figure 198 shows the equal rate lines for development. The time to bring the embryos to a certain stage is the same for a number of combinations of O_2 and hydrogen ions. Too low or too high hydrogen ion concentration has the same effect. The figure may be further interpreted as meaning the same result is obtained at optimum hydrogen ion concentration when O_2 is too low. Hall also found that low O_2 in combination with high hydrogen ion concentration retards the development of the toad. Jewell found similar results for the regeneration of tadpole tails.

3. *Higher invertebrates—Insects, etc.*

Stickney (864) found dragon fly nymphs quite indifferent to hydrogen ions. Water of pH 1.0 to 2.0 had little effect upon them; there

[3] If protoplasm has a constant or nearly constant pH—and there are reasons for believing that it does—and if oxygen is held and liberated by some protein, a pigment, of the egg protoplasm comparable to oxyhemoglobin and hemoglobin and having a comparable buffering effect, Hall's findings are what would be expected provided the lower pH (pH 6.2–6.6) was caused at least in part by a higher carbon dioxide pressure. (Barcroft, *Physiol. Rev.*, vol. 4, p. 330, 1924).

was much free mineral acid. Juday (461) found that Corethra does not react to hydrogen ions (221). Powers worked on crayfishes and found that H_2CO_3 had more marked effects than acetic acid.

4. Lower invertebrates

Hyman (426) found that acids added to carbonate free water had practically no effect upon oxygen consumption of Planaria. The effects obtained by adding acid to water containing carbonate are due to CO_2 liberated, indicating that CO_2 and not H ions is important. Clowes and Smith (185) studying fertilization, found pH the best index, CO_2 having no special effects. (625.)

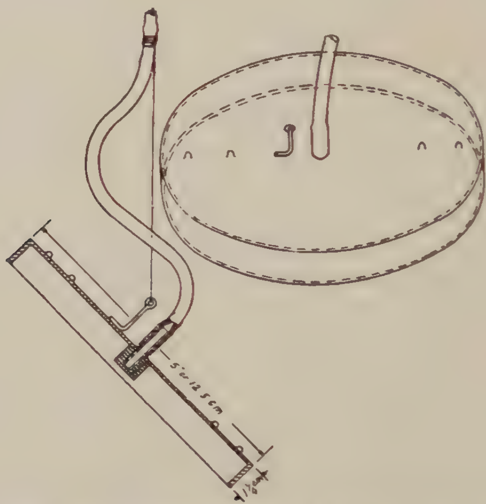


FIG. 199. A small pan to insure securing a sample from above the surface of the bottom.

IV. MEASUREMENT

1. General principles of chemical measurement in the field (822)

The first requirement is that the samples come from the place where the organisms live and be sufficient in quantity to make determination practicable, and still not disturb the conditions to such an extent as to make the sample non-representative. The manner of pumping samples illustrates the general principles and differences between the water chemist's and biologist's viewpoints. The water chemist, as a

rule, takes his samples from a fixed distance from the bottom or from a fixed depth (353) the purpose being to secure a record of the conditions of the water in general. The ecologist is interested in the open water especially from the viewpoint of plankton. So far as the bottom fauna is concerned, it is important that the samples for the determination of all the important factors come from the bottom. To accomplish this, Thompson[4] used a large flat plate with intake for the pump in the center. This collected much mud. The author designed a small pan with screen for small samples (fig. 199) which was tried by A. R. Cahn on the Wisconsin lakes. It consisted of a can-lid-like tin with a screen-covered intake which would ordinarily be 12 mm. from the bottom. For hydrogen ion samples only 5 cc. of water was used (from a depth of 10 meters) and the first 2 cc. were to wash the hose and tubes, the last 3 cc. being used for the determination of hydrogen ion concentration. An intake tube with a bore of little more than 1 mm. diameter was used for these small samples.

Samples for any and all the factors must be taken by the methods which give a representative collection for conditions in which the animals occur. The collections may commonly be much smaller than the 250 cc. ordinarily used. As little as 100 to 150 cc. is sufficient for most determinations of O_2, CO_2, etc., and 5 cc. for hydrogen ions. If much care is used the results will be more representative of the conditions, under many cirumstances, than larger samples made non-representative in the taking.

2. *Determination in the field*

a. CO_2 pressure. The probable value of CO_2 pressure determination lies in the fact that organisms are probably affected by all the forms of CO_2 (including ionization products) which exist in natural waters. From Johnston's work (453) CO_2 exists in water both as simple CO_2 and as H_2CO_3, the equilibirium being CO_2 (gas) $\rightleftarrows (1-n)$ CO_2 (dissolved) $+$ (n) H_2CO_3. The value of n is unknown, but is greater than 0.5; that is, over half of the CO_2 in solution exists as H_2CO_2 and less than half as unhydrated CO_2; but both probably have biological significance, which may explain the inadequacy of pH. The CO_2 pressure is conditioned by total $(CO_2 + H_2CO_3)$ in solution and there is no known method for obtaining the simple CO_2 fraction. Of the various methods for determining the CO_2 pres-

[4] T. G. Thompson, University of Washington, personal communication.

sure, Saunders' considers salt concentration and Powers' is suited to field work.

An *atomizer bulb*, barometer, small shaking funnel (U. S. Bureau of Animal Ind.), and for accurate work a tank of air of known CO_2 content, are the requirements in Powers' method, additional to the usual outfit for making pH readings. After the pH of a sample has been determined without contact with the air, it is thoroughly aerated and the pH read again. This second pH is called RpH (Marriott, (572)) meaning RESERVE pH, because it is a good index of the alkali reserve (of the blood). The method was devised for clinical use. If there were no other arguments in favor of this method, the fact that it gives two pH readings on a water sample instead of one, is sufficient to justify advocating it.

From the pH and RpH, Powers calculates the CO_2 pressure as follows: (1) the pH of the water determined without loss of CO_2 (2) the RpH (Mariott) of the water which is the pH of water after it is brought into equilibrium with the CO_2 of the air; [(2a) the ARpH of the water, which is the pH after the water is brought into equilibrium with alveolar air from a normal person (per cent CO_2 must be determined for the individual; varies inversely with the atmospheric pressure) brought about by blowing through the water, may be used as a check]; (3) the partial pressure of CO_2 in the air as known from the fraction volume is 0.0003 [the partial pressure of CO_2 in alveolar air (in fraction volume) is normally 5.5 to 6.8 per cent and varies with the individual]; (4) the ionization constant of H_2CO_3 which is $(K) = 3.04 \times 10^{-7}$; (5) the constant for the solubility of CO_2 in water $(k_{gas}) = 0.044515$ for pure water at 16°C.; and (6) n which is the rate of change of pH per unit change in $-\log(Kk_{gas}P)$.

Johnston's k_{gas} or (C) being solubility at a pressure of one atmosphere can be converted to solubility at 1 mm. Hg by dividing by 760, e.g., $\frac{0.0441}{760} = k_{gas}$ (with P in millimeters) which will be moles of CO_2 dissolved for each millimeter of CO_2 pressure. $K_{gas} \times P$ (in millimeters) = total CO_2 dissolved at a pressure of P in millimeters of Hg. The n of Johnston[5] is the proportion of total (free) CO_2

[5] The n of Powers is not the same. Furthermore the n of Power's earlier papers is not the same as the n of this chapter and his subsequent papers because he did not at first change from moles to mm. Hg.

Powers (see *Ecology*, ix, 364–368; July, 1928) has added a correcting factor e_1 which makes a slight difference to the results. His pH or RpH = $-[\log P + \log(Kk_{ga}) + e_1]$. This makes the equation essentially empirical.

existing in the form of H_2CO_3. It is always more than 0.5 for ordinary waters.

Powers' formula is as follows:

$$\text{pH [or RpH]} = -n \log (\mathrm{K}k_{\text{gas}}\mathrm{P}),$$

in which P is known from the air with which the water has been brought into equilibrium. With barometric pressure, e.g., 740 mm., the CO_2 pressure is 0.222 mm. Hg. If the RpH is known, then all the factors of the equation are known except n, and its value may be found. After the value of n is found, the original pH of the unaerated water may be used to calculate P which is the approximate CO_2 pressure of the original water being tested.[6]

Finally Powers' method may be expected to fail to give accurate results in the case of waters carrying an alkaline turbidity, or during active photosynthesis (conditions of "negative CO_2"—Birge and Juday (89, 90)) though the latter samples might be ruled out on account of their high pH (above 8.5). Powers' statement that the mass law holds *when equilibrium has been reached* is true, but in actual work the *velocities* of the reactions in attaining this equilibrium are important. Colloidal $CaCO_3$ dissolves too slowly to permit any true

[6] The constant k_{gas} varies with temperature and to a lesser extent with salt content; these variations, as given by Johnston, are large enough to be considered in applying the formula:

Values of k_{gas}; Johnston, (453)

TEMPERATURE	PURE WATER	1.17N (= 6.84 PER CENT) NaCl	3.44N (= 20.11 PER CENT) NaCl
°C.			
3.5	0.0672	0.0484	0.0270
12.0	0.0500	0.0367	0.0213
16.0	0.0441	0.0328	0.0193
25.0	0.0338	0.0260	0.0159
30.0	0.0297	0.0232	0.0142
40.0	0.0236	0.0185	0.0117

The value of K (for H_2CO_3) also varies with temperature, being 3.04×10^{-7} at 18° and having a calculated value (Johnston) of 3.39×10^{-7} at 25°. Perhaps this is small enough to neglect, though an example taken from Powers' paper (showing a CO_2 pressure of about 11.2 mm.) gave a 10 per cent difference in the calculated pressure depending upon which value was used.

equilibrium in carbonating waters excepting with aeration periods far too great for field work. Waters which are troublesome from these standpoints are rare.

The CO_2 pressure in exposed water is continually tending toward equilibrium with the atmospheric CO_2 pressure. While the pH alone tells nothing definitely regarding the CO_2 pressure in the water, in any one river system where the salt contents of the water do not vary rapidly, the pH values, that is, comparative values, do designate to a

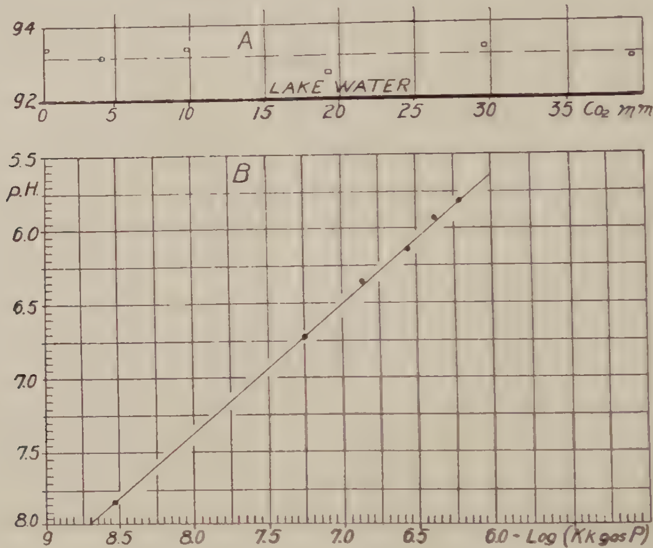


FIG. 200. *A*. Graph of the values of n in equation $pH = -n[\log(Kk_{gas}P) + e_1]$ of a clear water (Lower Lake) at different carbon dioxide tensions.
B. Graph of the linear relation between pH and $-\log(Kk_{gas}P)$ in a clear (Lower Lake) water. (692, 693, 694, 695, 696, 697.)

certain extent the comparative CO_2 pressures, provided that the dissolved salts and the temperature remain constant. The pH values of different river systems do not denote the comparative CO_2 pressures.

A stream or lake water which has a pH of 6.3 before aeration and an RpH 6.5 (after aeration) ordinarily has a low alkalinity. Pure water theoretically has an RpH of 5.68 (i.e., after aeration). In practice distilled water (aerated) has an RpH of about 5.0 or 5.5,

depending upon the amount of alkali dissolved from the glass container. Water with RpH above 5.68 is dominated by alkali. RpH below 5.68 indicates that a free acid dominates. Bog acid or acids may be present in any water, but not in a form which the physiologists call free acid, unless aerated water is below 5.68, at least theoretically. Powers (personal communication) has tested no water excepting bog water, where (when aerated) the RpH was below 5.68.

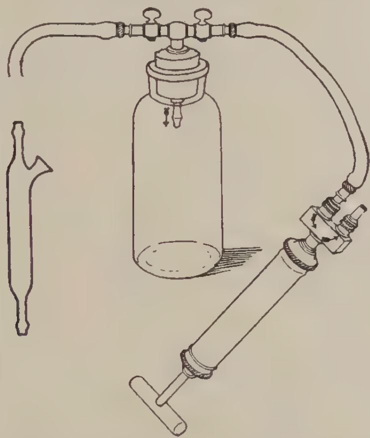


Fig. 201. Apparatus for securing samples with a minimum contact with the air. Water is pumped through the small tube, the size of which is the same as the colorimetric standards used, until the water in the 2-mm. lead has been thoroughly changed. The tubing is then clamped above and below the tube. The cork is removed from the side neck and the required amount of indicator introduced into the water with a graduated hypodermic syringe, or with a dropper. For very careful work the syringe must be used and for more careful work sheet rubber may be tied over the side neck and perforated with the hypodermic in inserting the indicator. After the pH has been read a small atomizer bulb and small injecting needle may be used to aerate the water and with care about three quarters of the sample will be left after aeration. The RpH may then be read.

H_2S or SO_2 in water is removed by aeration and the effect measured as CO_2. There is no objection to this, since they are not common. They occur only where oxygen is low, and oxidize rapidly into H_2SO_3 and then into H_2SO_4. CO_2 pressure as determined by the Powers method may be checked by the bubble or tonometer method wherever it is possible to take samples into the laboratory.

It is true that the determination of CO_2 pressure is a new and little

tried method as applied to aquatic habitats and aquatic animals. However, McClendon's results (552), Saunders' formula (775), and Powers' formula (696), are alike in that all indicate that the pH of an ordinary water has a linear relation to the logarithm of CO_2 pressure. Whatever proves to be in the value of CO_2 pressure measurements, the RpH is no doubt a valuable index of alkaline reserve or some other important property of a water. Data as to pH, RpH, and alkalinity which may be determined in the field quite readily, especially if Burroughs Wellcome tablets (p. 493) are used, can hardly fail to be of some value.

b. Hydrogen ions. The methods in common use are the colorimetric and the electrometric. The former is based on the colors assumed by solutions of various dyes in the presence of various hydrogen ion concentrations. Colorimetric standards may be color charts for rough work or for work on soils—those published in Clark's book (166) may be purchased separately—but for use in fresh water greater accuracy is necessary. For this purpose "buffer" solutions of known hydrogen ion concentration are placed in hard glass tubes, a standard amount of indicator added, and the tubes sealed and used for comparison with water samples with the same amount and kind of indicator added. Several firms make such sets of standards.[7] Standardization of buffers electrometrically is quite essential; also the purchased sets should be checked electrometrically at the beginning and end of each series of readings.

Thymol-blue (8.0–9.6), phenol-red (6.8–8.2) and the brom-thymol-blue (6.0–8.2) are among the most practical for use in the field as they do not fade on exposure to light. Brom-cresol-purple fades very quickly and should be avoided in field work. Saunders has shown (see his fig. 1) that brom-thymol-blue is least affected by temperature. Cresol red is best known as to salt error (709, 965). Saunders' figure 2 taken from Wells shows the magnitude of its value. Saunders has further pointed out that the salt error is dependent upon the difference in the normality of metallic ions in the solutions compared. Apparatus for the colorimetric determination of hydrogen ion concentration of very small amounts of fluid is available.

[7] Standards agree only with the brands of indicators from which they are made. The charts in the first edition of Clark's book agree with the Hynson, Westcott, and Dunning indicators, while those in the second edition agree with the LaMotte indicators, which are similar to the British Drug House indicators.

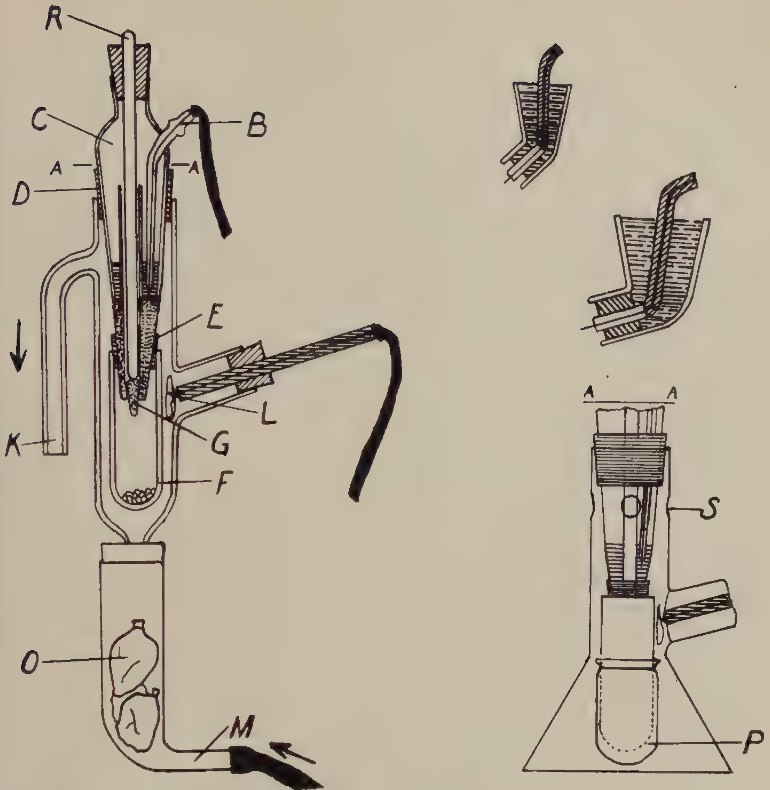


FIG. 202. Showing a quinhydrone cell (at left) for measuring the pH of a flowing liquid. The liquid to be measured flows in at M and out at K. The electrode, L, is a disc of 24 karat gold 2 cm. in diameter and 7 μ thick welded to a short piece of fine platinum wire. The wire is sealed in the glass tube, and mercury is used in the tube to make connection with the wire lead. The calomel cell, C, is designed to eliminate a flowing potassium chloride solution. Electrical connection to the cell is made through B, liquid connection to the gold leaf electrode is made around the ground-glass plug, G, and through the dense porous cup F. The glass rod R is in such position as to just touch G when the rubber stopper at the top of the cell is fitted tightly. This prevents the ground-glass plug from being raised accidently when the porous cup is being fastened on the rubber stopper, E, or by striking against the crystals of potassium chloride. Around the calomel cell is placed a section of large rubber tubing, D. The cell is rested on this rubber tubing in the top of the larger vessel. Thus the calomel cell can be readily removed for adding potassium chloride crystals to the cup or flushing with fresh solution. In service, the cell requires flushing about once a week, and the addition of extra crystals of potassium chloride to the cup may be made at the same time. The quinhydrone (purchased commercially or easily made) is introduced into the adapter in small silk bags, O, which require renewing about twice a week.

At the right is shown a modification of this cell below AA. See pages 492 and 496.

The so-called wedge colorimeter consists of two hollow wedges, one filled with the indicator of extreme acid color, the other of extreme alkaline color, and placed one in front of the other so as to make a solid of uniform thickness. The pH scale is then marked on the solid and a small celluloid tube is moved along the scale until a point at which the colors match is located. Great care must be used with colorimetric methods to check against fading, and against solution of the containers which changes the hydrogen ion concentration of the buffers, and against salt error. Electrometric checking of buffers and comparison with field tubes is essential.

Hydrogen ion concentration can be determined electrometrically in the field. The hydrogen electrode has been superseded as it was quite unpractical (361, 396). The quinhydrone cell or the tungsten cell may be employed. The former may be used for water of pH 9.0. The statement of 3.0 to 7.5 is very conservative. The range of the tungsten cell is from 5.0 to 12.00 but the difficulty of operation is considerable, and the cell does not have the accuracy commonly required in laboratory work.

Manufacturers are able to make a very compact field potentometer, etc., for reading the hydrogen ion concentration. See Parker and Baylis (643), Parker and Greer (644), and Biilman (86).

The quinhydrone dip cell (shown in connection with figure 202) has not been tried, but is suggested for examining natural water at various depths or the bottom (fig. 179 and p. 491). It makes use of some principles followed in the laboratory type of cell. Four holes, *S*, are provided, in the larger vessel of this dip cell, for outlets in place of tube *K* as shown in the laboratory type. The adapter is omitted and instead the quinhydrone is to be placed in a sack, *P*, fastened around the porous cup. The outer vessel flares at the bottom and is open to allow the water to flow around the sack, up and out of the holes, *S*. This entire apparatus should be fastened in a wire basket and weighted to insure an upright position at all times during the use of the cell in the water. The same care with regard to electrodes and chemicals would be required with this type of cell as is required with the laboratory type.

When dipping this cell into the water, thorough insulation of the electrodes is necessitated. This may be done by placing mercury cups over the electrode openings and filling the cups with vaseline (fig. 194). These cups may be fastened in place on the cell by means

of large tubing or corks, or the glassware may be blown to meet these requirements. For RpH it is practicable to pump and aerate a sample to be determined by the same method.

c. Oxygen. Samples for oxygen determinations must be collected and prepared with careful manipulation. In taking samples it is necessary to prevent reducing the pressure and to prevent all contact with the atmosphere. The best method is to connect the sample bottle in the intake line of a large bottle from which the air is exhausted by means of an air pump. There must be no leaks. The sample bottle should be immersed in water to avoid reducing the pressure. The intake must also be large enough to permit water to enter at a rate consistent with the working of the pump so as not to reduce the pressure. A careful technique must be developed.

In the field oxygen may also be estimated by means of colored glasses carefully selected to imitate iodine solution and marked in cubic centimeters per liter or in parts per million. This method should *never* be used where any other can be employed, i.e., only where the carrying and standardization of thiosulfate is impracticable. The standards below 3 cc. per liter should be in 0.25 cc. per liter.

d. Alkali reserve, alkalinity or buffer value (506). Acid titration methods are methods of indicating a measure of buffer value, or the ability of the water to neutralize acids or alkali. Some addition of an acid is essential to completely neutralize or nullify this ability. To determine alkali reserve in the field there are two principal methods:

Titration with standard acid and methyl orange is by no means free from difficulties, but in fresh water biology it is an important method. Methyl orange should not be used in waters containing aluminum and iron sulphates. For field determination of alkalinity, Burroughs Wellcome (962) water analysis sets may be used. Some sodium acid sulfate tablets ($NaHSO_4$) and methyl orange indicator are, however, the only actual requirements. A Wellcome tablet (0.324 gram) is dissolved in 50 cc. or more of water, in a white enameled dish, methyl orange introduced, and water added from a burette, or other measuring device.

The determination of pH colorimetrically is practicable, and CO_2 (titration method) can be estimated and the alkalinity determined with the use of the formula of Prideaux (700) or Greenfield and Baker or taken from figure 196.

e. Other chemical conditions. The gases and acids involved are H_2S, SO_2, ammonia, and methane. The last is non-toxic and appears to have no effect. Small quantities of ammonia (8 ppm.) are fatal. Sulphur dioxide is about half as toxic. H_2S is more toxic than ammonia. Traces of all these substances may occur in natural water.

Salts have important effects upon fishes (963), though no particular combination or quantity of the salts commonly in fresh water seems to prevent fishes from occurring. Their abundance may be seriously affected, however, and their presence may not indicate that they breed in a particular place. The non-carbonate salt content seems to be overshadowed by the CO_2 pressure carbonate equilibrium, the resulting pH and oxygen, or those conditions which are intimately associated with respiratory activity and decomposition.

The determination of SO_2 and H_2S is often necessary in experimental work. This is accomplished by adding a definite quantity of the water to a known amount of iodine without exposure to air, and then titrating back with thiosulfate. Salts must be determined by ordinary chemical methods.

Determination of total salts may often (in sea water and like waters) be determined by means of an hydrometer and tables such as Knudsen's or True's (909); some salts are easily estimated from simple titrations, as, for example, NaCl in sea water from titration with silver nitrate with potassium chromate indicator. The titration accounts for the chlorine only but in known waters the approximate concentration of particular salts may be derived from tables.

3. *Laboratory methods*

a. Oxygen. Apparatus designed by Thompson and Miller for determining the dissolved oxygen in water when only small quantities of the sample are available is shown in figure 203. Tube *F* is designed to hold from 3 to 5 cm. It may be calibrated with mercury. The amount of the sample necessary for the determination is just enough to fill *A*, *F*, and *J*, and is only from 5 to 10 cc. The procedure given herein is regarded as an improvement on that suggested by Lund, in providing greater convenience, more accurate control in the addition of smaller amounts of reagents, and complete protection of the sample from any possible contamination with the air.

The apparatus is connected, by means of rubber tubing at *A*, with the reservoir containing the water to be analyzed. Stopcocks *D* and

H are closed. The three-way stopcocks *E* and *I* are open so that the water will run up through *F*, and out through *J*. By the time *J* is filled, the sample of water in *F* will be free from any possible con-

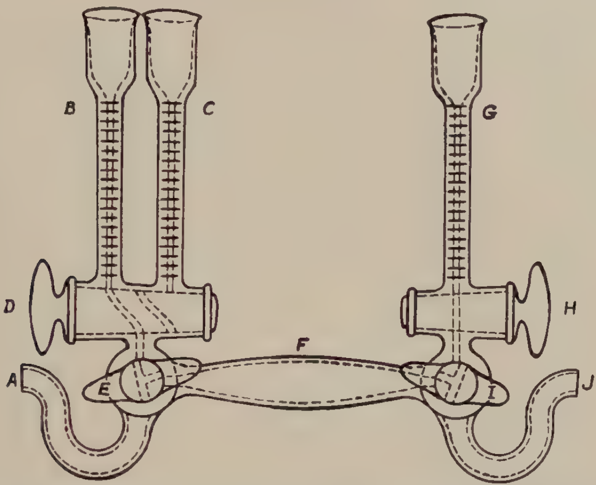


FIG. 203. Apparatus for measuring the oxygen content of small amounts of water by the Winkler method (Thompson and Miller, Apparatus for the micro-determination of dissolved oxygen. *Indust. and Eng. Chem.*, xx, 744–746, 1928).

tamination of air in the apparatus. Stopcocks *E* and *I* are then closed. Sometimes it may be more convenient to collect the sample by applying a gentle suction at *J*, while *A* is immersed.[8]

[8] *Treatment of sample with reagents.* The usual reagents for Winkler's method are prepared and used as follows: The graduated capillary *B* is filled with the manganese sulfate solution, *C* with sulfuric acid, and *G* with potassium hydroxide potassium iodide solution. *I* is then turned so that the sample in *F* is connected with the water in *J*. *E* and *D* are then turned so that the solution in *B* runs out into the water in *A* sufficiently to flush the capillary of stopcock *E*, and then by manipulating *E*, 0.02 ml. of manganese sulfate solution in *B* enters *F*. As 0.02 ml. enters *F* from *B*, 0.02 ml. will flow from *F* into *J*. *I*, *E*, and *D* are then closed. (ml. = cc.; footnote quoted.)

E is opened so that *F* and *A* are connected. *I* is then opened to *J*, so that the solution in *G* flushes the capillary in *I*, and then by adjustment of *I*, 0.02 ml. of the potassium hydroxide-iodide solution enters *F*. As 0.02 ml. flows into *F* from *G*, 0.02 ml. will enter *A* from *F*. *E*, *I*, and *H* are immediately closed. The apparatus is slowly rocked back and forth to permit mixing of the reagents in the sample, with the resulting formation of $Mn(OH)_2$ and $MnO(OH)_2$, the latter being formed by reaction of the $Mn(OH)_2$ with the dissolved oxygen.

For use with flowing water very low in O_2, Powers devised a special bottle which prevents all contact with air in dissolved oxygen free water. The reagents are introduced through a three-way cock from tubes calibrated in cubic centimeters (p. 520).

b. Hydrogen ions (166, 595, 641). Electrometric methods have hitherto been difficult because of bubbling hydrogen used in the hydrogen electrode. The quinhydrone electrode offers possibilities. It eliminates the use of bubbling hydrogen which pumps the carbon dioxide out of the water and thus changes the pH. The flow type electrode is shown in figure 202 and is drawn from a Leeds and Northrup instrument.[9] It may be substituted for the hydrogen electrode in the potentiometer apparatus so frequently described. It has the advantage of making continuous recording possible. Gesell (328a) has

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I is adjusted to connect *J* and *F*. *D* is turned to allow the sulfuric acid in *C* to flush the capillary of *E*, and then the latter manipulated so that 0.02 ml. of sulfuric acid is allowed to enter *F*. *D*, *E*, and *I* are closed and the apparatus is slowly rocked back and forth until the precipitate in *F* has dissolved. *H* and *I* are opened to *J*, and the tube *G* is washed several times with water and then with a dilute solution of sulfuric acid until the potassium hydroxide in *J* has been neutralized.

If too much acid has been admitted to *A* it is well to flush it out by pouring water through *B*; otherwise the apparatus is tilted so that *G* is uppermost. *E*, *I*, and *H* are adjusted so that the solution in *F* runs out through *A* into a porcelain dish. *F* and *A* are rinsed by running water in through *G*.

The liberated iodine is titrated with 0.002 N sodium thiosulfate, using a microburet and freshly prepared starch as an indicator. The thiosulfate solution is rather unstable, but its stability may be increased by adding a few drops of carbon disulfide to the reservoir and by keeping the solution out of contact with the air.

The thiosulfate solution may be standardized by using (a) a dilute standard iodate solution, to a measured quantity of which are added several drops of 6 N sulfuric acid and a small crystal of iodate-free potassium iodide; or (b) measured quantity of a dilute standard copper sulfate solution, treated with a small crystal of potassium iodide. In either case the liberated iodine is titrated and the normality of the thiosulfate solution determined.

Should the amount of iodine liberated in the oxygen determination be very small, the colorimetric method proposed by Lange and Ward, using o-tolidine, may be used. Cocks must be thoroughly greased for storage.

[9] The tracing of the flow type cell, (fig. 202) was made from a photograph supplied by Dr. H. C. Parker of the research department of the Leeds and Northrup Company and the material here presented, corrected and approved by him, though the suggested dip cell has never been tried.

recently adapted the quinhydrone electrode for determinations in small samples without loss of CO_2.

The recording of hydrogen ion concentration has been accomplished with the Leeds and Northrup potentiometer. Usually a flow type of electrode has been used. No doubt the current of a stream could be made to produce sufficient flow for the determination, but in ponds or other quiet waters a pump might be necessary. These recorders are readily adaptable to the taking of pH and RpH. In a two-point recorder the water in one cell may be aerated, while that in the other is not, making possible the essentially continuous recording of CO_2 pressure.

c. Free and total carbon dioxide, and carbon dioxide pressure. Free carbon dioxide may be determined by titrating to pH 8.0 with standard alkali. This is usually done with phenolphthalein by securing a faint pink which disappears in three minutes. The same precautions must be used to prevent contact with air as in the case of oxygen samples. Barium hydroxide may also be used. This, of course, is not an index of the CO_2 pressure acting on the animals.

Total CO_2 may be measured with the Van Slyke apparatus. The Van Slyke apparatus shown in figure 204 (918) is designed in proportions especially adapted to determination of CO_2 in blood plasma but was enlarged by McClendon for use with sea water (551). It consists essentially of a 50-cc. pipette with three-way cocks at top and bottom, a 1-cc. scale on the upper stem, divided into 0.02-cc. divisions and heavy-walled rubber tubing with a levelling bulb filled with mercury. The apparatus is made of strong glass, capable of holding the weight of the mercury, and is held in a strong screw clamp, the jaws of which are lined with thick pads of rubber. In the calibrated upper stem of the pipette 1 mm. of length corresponds to 0.01 cc. By estimating tenths of a 0.02 cc.-division, gas volumes can be read to 0.002 cc. To justify such readings the apparatus should be accurately calibrated as follows: Attached to the outlet at the bottom, is a short glass tube drawn to a capillary tip. This is to fill the apparatus by suction with distilled water as far as bottom of cock *e*. By use of cock *f* water may be drawn off, 0.1 cc. at a time, and weighed. The cocks should be held securely in place, against the pressure of the mercury, by use of rubber bands or similar elastic cords.

To test the instrument before a determination is made, the entire apparatus, including upper capillaries, is filled with mercury. The

mercury bulb is lowered to position *3* so that a Torricellian vacuum is formed. The bulb is again raised, and, if apparatus is tight and gas free, the mercury will refill it completely and strike the upper cock with a sharp click. Any gas in the apparatus serves as a cushion. If the click is not heard, a bubble remains above the mercury. This gas must be removed.

To make a determination, fill the entire apparatus, including upper capillaries, with mercury and wash the cup at top with carbonate-free ammonia to remove any acid. McClendon used it for seawater (551).[10]

[10] By means of careful manipulation of a pipette and the upper stop-cock, 10, 15, or 20 cc. of sea water are admitted, care being taken not to admit any air. It is permissible to leave one or two drops of this sea water in the 1 cc. cup at the top as this amount may be washed down by the introduction of 1 cc. of 2 N HCl in the same manner. A drop of mercury is placed in the cup to seal the stop-cock and the bulb lowered until the mercury falls to the etched mark near the bottom of the 100 cc. chamber. The lower stop-cock is closed and the apparatus is shaken laterally in the vertical position as vigorously as possible for two minutes (in case 20 cc. of sea water was used, four minutes). The sea water is now trapped off in the trap, T, and the mercury allowed to rise in the 100 cc. compartment until atmospheric pressure is attained in it and the lower stop-cock closed. At the end of one minute the amount of sea water above the mercury in the 1 cc. gas burette is measured, calculation being made for the two menisci. The apparatus is laid on its left side on a cushion and agitated one minute after the air is in the wide portion of the 100 cc. chamber. The apparatus is then clamped upright, the lower stop-cock opened, and the mercury levels are adjusted by means of a screw. The air volume in the 1 cc. burette is carefully measured. 1 cc. of 0.5 to 1.0 N NaOH is admitted from the cup into the gas burette to absorb the CO_2. In leveling the bulb to measure the gas residue, one-thirteenth of the height of the NaOH is reckoned as mercury. The total CO_2 that was in the original sea water is that absorbed plus that in the sea water above the mercury plus that in the sea water trapped in the trap, *T*. After these are calculated by means of the volumes, absorption coefficient, and CO_2 tension, they are added together and reduced to 0° and 760 mm. To do this it is necessary to know the barometric pressure and the capillary depression in the gas burette, which latter is subtracted from the former.

In the following example on 10 cc. of 0.576 N sea water at 20°, the absorption coefficient for CO_2 was 0.757, the barometric pressure 754 mm., and the capillary depression 2 mm. The CO_2 absorbed was 0.405 cc. and the gas volume before absorption 0.59 cc., making the CO_2 tension 0.687 (unity = barometric pressure). The sea water above the mercury was read as 0.075, to which was added the volume of menisci (0.0133) making 0.0883. The CO_2 in this sea water was $0.0883 \times 0.687 \times 0.757 = 0.0459$, which added to the absorbed CO_2 makes

With a pipette put the solution to be analyzed into the cup. When the solution contains some free carbonic acid as well as carbonate, the

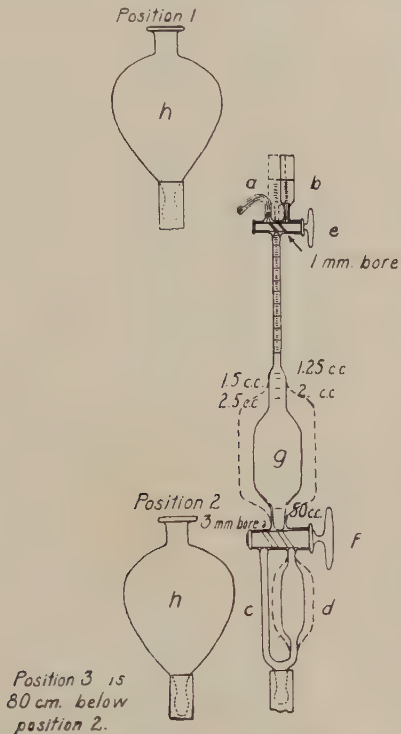

FIG. 204. The Van Slyke apparatus for determining the carbon dioxide tension in fluids (918). *a* is for the discharge of fluids through cock *e* from chamber *g*; *b* is to hold and deliver the fluid to be tested through cock *e*; to pipette bulb *g* which holds chiefly mercury. It is in *g* that the vacuum is produced by withdrawing mercury into *h* through cock *f*; *d* is for the withdrawal of fluids. The positions of bulb *h*, necessary at different stages in a determination, are indicated. The dotted outline indicates the enlargements made by McClendon (551, 552).

0.4509. This occupied a space of 89 cc. over 11 cc. of acidulated sea water; hence there is in the trap $\frac{11}{89} \times 0.4509 \times 0.757 = 0.0422$, which, added to that already calculated, makes a total of 0.4931 cc., and which, reduced to 0° and 760 mm., is 0.442 per 10 cc., or 44.2 cc. per liter. Since the pH was 8.2 and the alkaline reserve 25, the total CO_2 agrees with figure 195.

When not in use, the entire apparatus should be filled with water, cock *c* properly greased. The mercury occasionally should be cleaned by straining through chamois skin.

tip of the pipette must dip below the surface of the solution in the cup during the transfer. With mercury bulb in position *2* and cock *f* as shown in figure 204, admit solution from cup into the 50-cc. chamber, leaving enough above the cock to fill capillary *b*. Wash cup twice with 0.5 cc. of water each time, finally running in 0.5 cc. of 5 per cent H_2SO_4. After acid is admitted, a drop of mercury is placed in *b* and allowed to run down the capillary as far as the cock in order to seal the latter. Wash out excess H_2SO_4 in cup with water. Lower mercury bulb to position *3*, producing a Torricellian vacuum in apparatus. When mercury meniscus is at 50 cc.-mark, close lower cock, remove pipette from clamp and turn upside down fifteen or more times to agitate contents. Replace in clamp. Turn lower cock and allow water solution to flow into *d* without any gas following it. Raise levelling bulb with left hand, and with right hand turn cock so as to connect pipette with *c*. Place mercury bulb at such a level that the gas in the pipette is under atmospheric pressure and read the column of the gas on the scale. After finishing determination, lower levelling bulb without opening upper cock, until most of the mercury is withdrawn from pipette through *c*. Readmit water solution from *d* and raise mercury bulb to position 1, thus forcing water solution with a little mercury out of apparatus through *a*.

V. CONTROL OF CHEMICAL CONDITIONS

1. Oxygen

Oxygen content may be controlled by boiling and cooling or by adding oxygen from tanks. Usually the boiling may be accomplished in glass, if the water is allowed to run slowly in and out of two boiling flasks. It may be cooled in tubing surrounded by cold water. It is practically necessary to keep such water running over the animals to insure lack of oxygen.

In boiling the O_2 out of water (89), all the "free" CO_2 is boiled out, and usually when all oxygen is removed pH 8.5 to 9.0 is reached. At pH 9.0 the carbonates usually begin to precipitate in water and may make the water cloudy at alkalinity 140 parts per million of $CaCO_3$. This is too alkaline for most experimental purposes. A quantity of acid must be added to bring the water to pH 7.5 or any desired condition. Acid may be introduced through the device shown in figure 205 which gives nearly constant flows over considerable periods.

Oxygen may also be removed by bubbling hydrogen or nitrogen

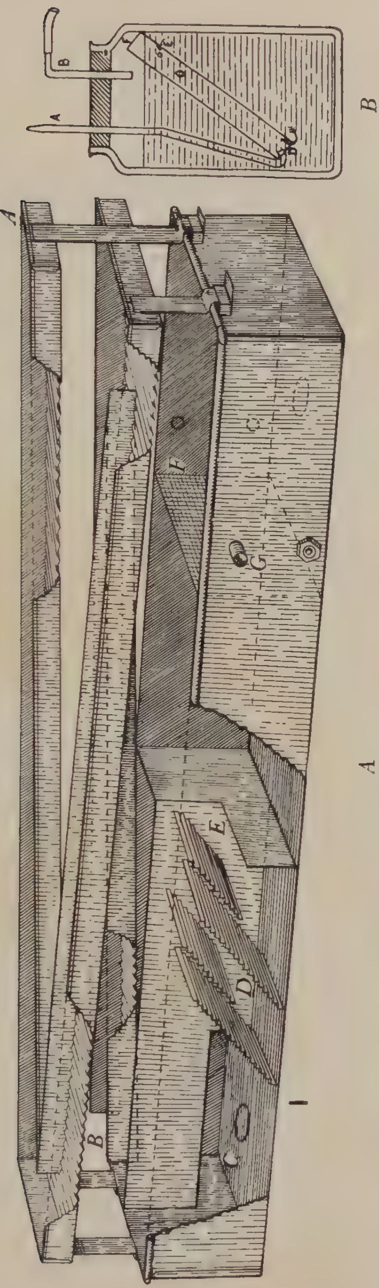

FIG. 205. Aerating devices. *A*, for running water; *B*, Allee's device for aerating water without disturbing it with bubbles. The bubbles pass upward through a tube escape to the surface but carry a current of water up and out of holes in the side of the tube. May be used with a filter pump or compressed air.

through the water or by exhausting the air from the water. The latter is a very practical method (see Chapter XX).

2. Carbonate free water

This may be made by adding HCl until the carbonates are all converted into chlorides (at pH 4.0). Compressed air, preferably ammonia free, is then bubbled through the water to pump out the CO_2. Excess HCl is to be avoided as even boiling will not remove it. Carbonate free water does not become alkaline when the dissolved oxygen is boiled out. Carbonate free water is essential in the study of the effects of hydrogen ions. Gases such as O_2, CO_2, SO_2, H_2S, etc., may be added to water by simply bubbling them through it. Allee's device for preventing general disturbances of the water and for maintaining circulation is shown in figure 205 (11). Tanks of compressed gas with pressure reducing valves are essential. Inverted bottles may be used, and gas displaced with water (fig. 204). (See also page 242.)

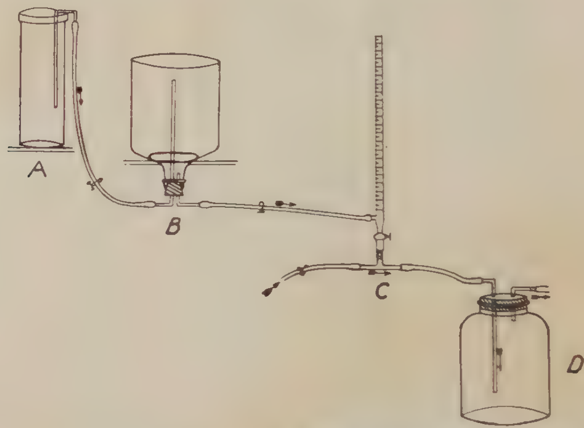

FIG. 206. A system of vessels for adding gases to water from inverted bottles. Water is slowly siphoned into *B* from *A*. Entering *B* it flows over the long tube exposed to the gas and flows slowly out into the burette and flows drop by drop from the burette tip through a bubble of air in the upright arm of a tee in the running water supply of the experimental bottle *D* (after Wells, Bulletin Illinois Natural History Survey).

CHAPTER XX

The Location and Planning of Buildings and Equipment for Simulating Aquatic Conditions

I. INTRODUCTION

The reproduction of natural conditions for aquatic life has long been the aim of various show aquaria, such as the New York Aquarium and the Aquarium of the Naples Zoölogical Station. The use of running water is already an ancient practice in fresh water aquaria and park pools. The water is kept at a temperature compatible with the life of hardy species. The animals in them, as a rule, have lived in part on the life suspended in the water and in part on food supplied artificially. An ideal aquatic "climate"-simulating laboratory should improve upon the experience of workers in aquaria and at the same time utilize the practices of the existing aquatic biological laboratories. In general, the aims of such a laboratory are different in many respects from those of the existing aquatic biological laboratories. The majority of these function as teaching centers in the summer months and as places where one may go for a few weeks or at most a few months to carry on investigation, important often to a high degree but desultory and unorganized in its general purpose and especially in its demands for equipment. The investigator seeks "material" with which to test a particular physiological hypothesis or embryological theory. He wishes, for example, to keep his animals alive for a short period of development or regeneration, or to secure a set of readings on metabolism. The results in the form of records and preserved material are taken back to his college laboratory for study and publication. In the main, the aquatic laboratories of the world are organized to accommodate this type of investigator. A few, however, such as the station at Plymouth, England, at Lenz, Germany, and possibly the Volga Station, the Scripps Institute at La Jolla, California, the United States Bureau of Fisheries Laboratory at Fairport, Iowa, which was designed primarily to study the culture of bottom mussels, have programs of investigation and regular staffs. There is in other words very little in the way of facilities similar to the extensive Agricultural Experiment Stations on land.

II. STATION SITES AND WATER SYSTEMS (190, 488, 942)

The primary aim of the summer laboratories is not to duplicate natural conditions but to keep the animals alive for a period long enough to permit the making of the desired observations. The maintenance of the normal temperatures, oxygen and hydrogen ion content, etc., in the water circulated to the laboratories has been a minor consideration. Especially the plankton and other conditions of nutrition, such as detritus, have been neglected, as is indicated by the frequent use of recirculated filtered water.

A suitable supply of water is the first consideration in the locating of an aquatic "climate" simulation laboratory.

The chief difficulties in keeping animals alive probably have been due to:

1. Lack of oxygen in the water,
2. Poisonous decomposition products, including CO_2,
3. Super-saturation with nitrogen,
4. Poisons from metals in pumps and pipes where water was recirculated, and
5. Parasites and diseases.

The two leading descriptive accounts of fresh water and marine laboratories, by Kofoid (488) and by Ward (942) give description of the aquaria, pumps, and water source, methods of storing and recirculating water. It is evident that this subject has long ago progressed somewhat beyond the present status of climate simulation for small land animals.

1. Source of water supply

Fresh water supplies in laboratories are usually the city water, impounded by damming streams, or pumped from a lake or river or from wells. They are frequently chlorinated, which renders them very poisonous to animals (814, 816, 819). The suspended earthy matter is commonly removed by filtering, settling, or chemical treatment where necessary. Well waters are often very hard. In the Mississippi Valley they frequently contain much iron and CO_2. Gases such as methane and other illuminating gas constituents may be present. Oxygen is nearly always deficient in well waters and sometimes entirely wanting. They frequently contain salts that have ill effects upon animals and plants.

Fresh waters brought from elevated dams or lakes may also be undesirable for animals. This is particularly true if the source supports a rich plankton or a rich flora and fauna. The period of darkness in the mains frequently is sufficient to kill everything and produce considerable CO_2, an odor of H_2S, and to consume all the oxygen. No city water supply, therefore, can be trusted to be suitable for biological work. Chemical analysis and biological tests must be applied before use is made of it. For biological tests young fry of trout or other sensitive fish will serve fairly well (Shelford (816)). However, in spite of the statements above, some cities, such as Portland, Oregon, have municipal supplies hardly to be improved upon. Any water supply coming from a high altitude and resulting from melting snow and ice is likely to be good. It enters the aqueduct with a large oxygen content, a small plankton and small organic content.

Most biological stations are located on unpolluted rivers, lakes, or the sea, and supply their own water to ponds and aquaria. Very few of these, however, have had as their aim the conducting of experiments on the effects of aquatic conditions or on the continuous breeding of animals. Usually their aim has been to keep animals alive and in a healthy condition during the progress of short-period experiments.

2. *Pumping and treatment* (274)

The method of handling the water for short experiments or any other purpose is largely dictated by the character of the source. If the source is variable in character, storage is commonly resorted to and recirculation often practiced. Variability of the sources is commonly due to (1) floods or on-shore winds resulting in mud sediment, (2) growth of algae or plankton in much greater volume than average, and (3) periodic entrance of polluted waters into the source of supply.

One prerequisite of an aquatic station site is a water as nearly uniform throughout the year as possible and with an approximately normal annual cycle of planktonic events. Where such a water supply is not available during these unfavorable periods, viviers, such as are a part of the equipment of several French stations, can serve this purpose. There are two fundamentally different methods of supplying water. They may be separated on the basis of the content of living things and their sensitivity to changed conditions. When water is pumped and stored in ordinary tanks or held in the mains for some time, the changed conditions, such as a rise in temperature, lack

of light or lowering of oxygen content, kill some of the plankton in a short time, and the consequent putrescence in turn kills most of the animals and plants remaining in the water. The micro-flora and fauna of water stored and recirculated is unlike that of the water pumped or other natural water. This is well illustrated by the following comments of Allen (25) on the stored and recirculated water at the Plymouth station:

Tank-water, or water taken from the supply of sea water circulating through the tanks of the aquarium at Plymouth, shows some striking and interesting differences from "outside water." This water is pumped up from the sea, just below the Laboratory, into two large, covered-in, settling reservoirs, with a capacity of 50,000 gallons each. Pumping is done only at high water, spring tides, so as to get the least contaminated water, and no water is pumped that does not show a specific gravity, measured with a hydrometer, of $\rho^{17.5} = 26.00$ ($S = 34.00$) or over. The water is allowed to settle for about a fortnight before being used for the general circulation.

The tanks themselves are made of slate and glass, and the pipes which convey the sea water to them are of vulcanite, so that the water does not come in contact with metal, excepting in the pumps, which are of cast-iron. The two settling reservoirs are used alternately, for about a week each. From time to time, tide and water allowing, waste is replenished, and about twice a year each reservoir is emptied, cleaned out and refilled. The aquarium takes about 20,000 gallons, and this is in circulation with one of the two 50,000-gallon reservoirs. An estimate of the amount of life in the tanks of the aquarium must be exceedingly rough, but the intensity of the larger forms of life is far greater than anything met with in natural waters. About 500 fish and 2000 invertebrates, including all forms as large as an *Actinia equina*, might be somewhere near the mark. So it will be seen that the accumulation of excretory products must be a by no means negligible factor. The flora of the tanks is very restricted, and is chiefly composed of minute forms of algae. Minute naviculoid diatoms, *Ectocarpus*, *Cladophora*, *Enteromorpha*, *Vaucheria*, and unicellular algae are the commonest forms. The large seaweeds, such as *Fucus* and *Laminaria*, do not live long if introduced. Plankton diatoms, although a great number must be pumped up when the reservoirs are being filled, are not represented.

The main difficulties with the water supplies of these laboratories lies in the fact that they have not been lighted. In an attempt to keep the temperature from rising, to prevent evaporation, dilution by rain, the tanks of laboratory water supply have been put below ground or covered and accordingly kept practically in darkness.

A second frequent practice is filtering the water. This no doubt removes objectionable matter and excreta but it also removes the normal life of the water.

The storage and recirculation of rain water as carried on at the University of Illinois illustrates another difficulty. The water is stored in a cistern of ordinary construction, pumped onto sand and filtered, and then carried to an attic tank from which it is run through the aquaria and back to the filters. The water had an alkalinity of 90 parts per million on one occasion and a few months later had risen to 300 parts per million. In other words, the dissolving of inorganic salts is a source of difficulty with recirculated water. The same amount of expense in treating the regular water supply by means of

FIG. 207. Showing the arrangement of land, buildings, etc., of the Puget Sound Biological Station. *T*, tank; *P*, pump; *O* and *V*, vivier (488) as shown in figure 208.

aeration and filtering would probably be more economical and lead to more satisfactory results.

a. Methods of supplying water by pumping. There are three methods of providing adequate water supply by pumping. (a) One is direct pumping from a uniform source in which the water reaches the point of use in a few moments. (b) Another consists in storing the water in deep reservoirs open to the sun until self-purification can take place and a flora and fauna suited to the conditions of the reservoirs can be developed. (c) A third involves storage with cooling by a refrigeration machine and an internal circulation

and possibly aeration to keep the water temperature normal and maintain the normal fauna and flora during storage.

A plan for a constant pumping water system has been proposed for the Puget Sound Biological Station (figs. 207 and 208). *P* is the pump house on the main channel shore where tide passes at a maximum of 4 to 6 knots per hour. It contains two centrifugal pumps with motors directly above the centrifugal pump shafts. They are mounted on a floating platform which rises and falls with the tide. The platform is inside a square concrete enclosure with heavy iron gratings and cross plank doors which may be lowered in bad weather

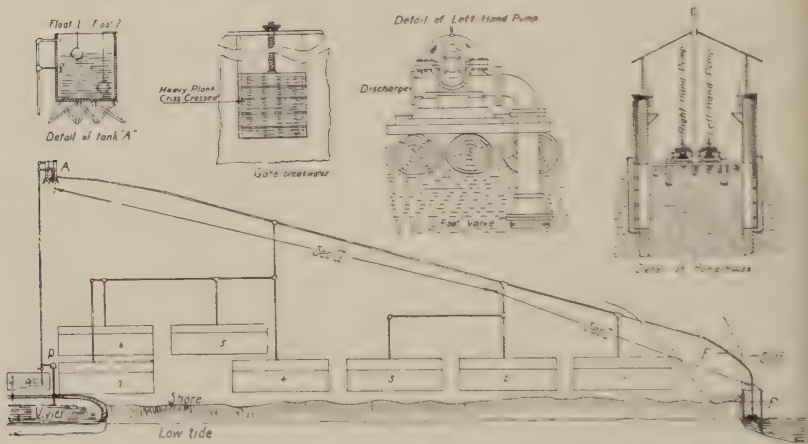

FIG. 208. Diagram of water-pumping system proposed for Puget Sound Biological Station. *P*, pump; *F*, flexible pipe; *A*, small tank; *p*, bad weather pump; *a*, aquarium; *1–7*, laboratories.

but which will admit water through a number of 1 cm. openings left by the cracks between the planks. The rise and fall due to the tide is permitted by the use of a universal pipe joint and 25 meters of flexible hose. The water pumped is forced into the main of $1\frac{1}{4}$ inches (31 mm.) pipe, which passes up the hillside above the station to a height of 21 meters above low tide and ends in a small tank 2.6 meters in height to the top overflow and 2.3 meters in diameter. The 13 mm. overflow is 0.5 meter below the top overflow. This connects with a pipe leading directly down the hill to a show aquarium (*a*) with glass sides.

The laboratories arranged along the shore at an average of 6 meters

above low tide are supplied from the main with an average head of 15 meters, which is maintained by a ball float which starts the second pump. There is a head of 3.3 meters above the pipe leading to buildings. When the pressure falls below this due to the lowering of the water, the second pump is started. If the two pumps deliver more water to the upper tank than can flow out of the small outlet, it rises and thus raises the ball float and turns resistance in series with the first pump and decreases its speed. As soon as the rapid withdrawal of water is reduced the first pump is started at full speed and the second pump stopped. The purpose of the one variable-speed motor and the stopping and starting devices is to give flexibility. The plan proposed to provide for 150 3-mm. ($\frac{1}{8}$ inch) openings with considerable margin. If only two or three of these happen to be open the small tank will be filled and the first motor slowed. If the level in tank *A* falls below float 2, it starts the second pump. This plan has not been put into effect but there is no doubt that it can be made to work successfully within the limits of continuity of electric current supply. The chief source of danger lies in the automatic starting of the second pump. Some device by which the water standing in the pump can be disposed of must be provided as it is this which is likely to be contaminated with metals and injure animals under experimentation in the research laboratories. Where the second pump starts at intervals of a few hours there will be no trouble if a simple device is installed in order to turn a three way valve which discharges to the exterior at the beginning, and later into the supply line. This can probably be developed either using water pressure or electricity. If the peak load does not come too often, manual operation to clear the pump of standing water a short time in advance, can readily be accomplished.

Centrifugal sump pumps as shown in figure 209 are to be preferred to those with foot valve in figure 208. The sump pump if used must be very rigidly fastened, as the alignment must be perfect if the pump and motor are not to become rapidly inefficient and wear out quickly. The difficulties cited are by no means insuperable and the direct pumping method is to be preferred wherever practicable.

In bad weather a small gasoline pump can be made to draw the water from the concrete vivier—in the opposite direction through the pipes. Bad weather in this area is rare outside of the winter months. The vivier should be provided with tight gates to large openings which may be closed in bad weather to keep out silt.

One advantage in such a system is that the pipe to the first or second research laboratories numbered *1, 2, 3* in figure 208 may be of any desired nonsoluble material, leaving the pump and a short length of pipe the only metal exposed.

3. Effects of metals (488)

The effects of metals in poisoning water used for biological work no doubt have been greatly exaggerated. The difficulties were probably

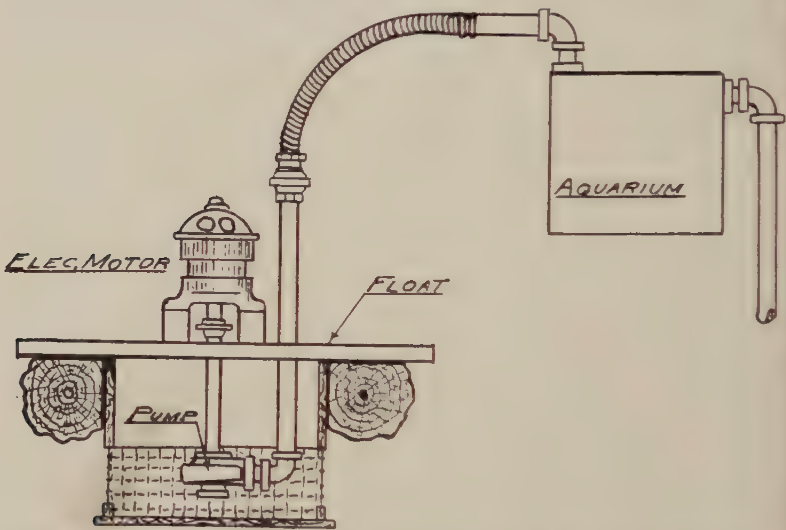

FIG. 209. Sump pump for continuous service into a line carried on a float with a heavy rubber hose.

due to changes during storage, and the death and decomposition of animals, the lowering of oxygen content and the rising of CO_2 content. Where water is recirculated and remains in contact with metals for long periods they may have a bad effect. The worst source of contamination likely to affect the investigation is the dead end of pipe on which cocks are closed for some time. In any system it is wise to make the stubs bearing the cocks of hard rubber, unless the users can be depended upon to open the cocks for a time before using the water. A surprisingly large number of stations use pumps and pipes made of metal other than iron. Those observed by Kofoid were at the following stations. The running water systems at Naples were soft lead,

the pump at Monaco was phospher-bronze, also the same at Villefranche and Alte. At Argon the sea pipe is copper, the pump bronze, and the laterals are of lead and the cocks hard rubber. At Concarneau, the station of Delage, the pump is brass, the laterals lead, and the valves and cocks of brass. Arrangements are similar at Roscoff. In the Plymouth station, however, iron and rubber are used but terminal cocks are brass. On the other hand, the galvanized pipes and brass valves and cocks are used at Port Erin where the aquaria are "among the most thriving in European stations."

4. Storage in light

The storage of sea water without temperature control is practically accomplished at the Roscoff (France) Station (488).

The vivier of the station is specially arranged for biological purposes. It serves as a reservoir from which the water for the station is pumped and as a storage basin for large animals and for animals under culture or observation. It is a square basin (about 36 by 36 meters) with rounded outer corners jutting from the shore seaward, containing nearly 1,000 square meters of surface. A heavy wall of masonry, 4 meters thick at the base, forms its outer boundary. On the inner side of this wall is a reënforced concrete platform, 4 meters wide, supported by pillars of the same material. The faces between the pillars are closed above the water level by doors of tarred planking, thus forming a dark gallery, 70 meters long and 4 meters wide, where shelter-loving, fixed animals readily develop under quite natural conditions. The bottom of the vivier is made of concrete and slopes from the margins (3.5 meters) to the gate (4 meters), facilitating the cleaning when necessary and insuring the retention of the water at times of low tide.

From the vivier a cement conduit, 0.8 meter in diameter, extends seaward for about 100 meters to a point near low-tide level. By means of this the vivier can be filled at the high tide with pure sea water from the channel relatively free from shore contamination. The conduit is closed with an iron gate regulated from the platform by a screw. The openings were too small, and poor circulation is reported to have interfered with the success of the vivier through the accumulation of silt.

The marine park is situated between the Isle Verte in front of the

laboratory and the vivier, at some distance from the island on a rocky strand exposed at low tide. It is set aside under the exclusive control of the station as a collecting ground where continuous observations may be made on animals in a natural habitat or where cultures may be conducted. It is a rectangular area 25 by 50 meters inclosed in a wall of loose granite rocks and containing many rocky shelters for the protection of the fauna.

A unique feature of the equipment of the Concarneau station is the large vivier, a group of large culture basins extending seaward from the south face of the laboratory. The shore has been excavated and the sea front of the basin extends to low-tide level. The vivier is surrounded by a massive outer wall of granite whose lower part is 1.8 meters thick and 4 meters high. Upon this rises a protecting wall 2 to 2.4 meters above high-water level, to prevent damage to the basin by the storms to which it is exposed. The vivier, which contains about 1,350 square meters, is subdivided into eight basins of different sizes separated by partition walls of granite 0.9 to 1.4 meters wide, whose tops serve as walks about the vivier. The open spaces are in part sheltered from the direct rays of the sun by loosely laid wooden covers. The vivier connects directly with the sea by a gate adjusted by lever and screw to regulate the inflow and outflow of tidal waters. Gratings in the partition walls permit the free circulation of the water between the several basins of the vivier. The basins were originally intended for use in pisciculture, and especially in lobster culture. They serve at present as storage basins for fish used in obtaining ova for hatching experiments and for storage of material obtained on collecting expeditions. A very considerable quantity of the normal shore fauna develops upon the rocky bottom and walls of these basins and is thus readily accessible under all conditions of weather to the naturalists at the station.

The use of refrigeration to keep water cool has not been practiced so far as we know. It is for sea water that this could be most profitably employed.

At the Fairport Station of the United States Bureau of Fisheries (190, 192) water is stored. The crude river water of the Mississippi at this place contains the necessary elements for the life of fish and mussels, and after standing in the earth ponds, under the active influence of sunlight and vegetation, it develops a rich stock of food to form a peculiarly favorable condition for fish life.

The pumping equipment consists of two 60-horsepower return tubular boilers and three steam turbine-driven centrifugal pumps. The two larger pumping units are of 40 and 20 horse power and have capacities of 5,300 and 3,280 liters per minute, respectively; the crude river water is delivered through a main of 35 and 30 cm. pipe to the storage reservoir, from which there is a gravity flow to the ponds, to the tank house, to the basement of the laboratory, and to the temporary laboratory, which has been converted into a hatchery.

The storage reservoir for river water has, in approximate terms, an area of nine-tenths of an acre, a depth of 4.5 meters at the outlet, and a capacity of 7,570,000 liters. The reservoir allows opportunity for sedimentation of the coarser particles in the river water and for the development of the elements of fish food. While pumping operations are usually carried on for five to eight hours each week day, the capacity of the reservoir makes it possible to discontinue operations in case of emergency for two or three days.

Attention has already been called to the fact that many experiments on fresh water animals must be carried on in natural waters running over earth bottom where reproduction can take place and the animals kept under natural conditions. Some of the various plans for fish ponds fed by streams can be modified to meet these conditions. One of the greatest difficulties results from floods which may call for impounding reservoirs such as those at Fairport to be used temporarily while flood waters are diverted altogether.

III. THE REMOVAL OF SUSPENDED MATTER

The removal of matter suspended in water should usually be accomplished by settling (see above description of the Fairport Station) as this method favors a large growth of plankton and small organisms which are usually an important part of the environment of aquatic animals.

Filtration removes much of this and is, therefore, undesirable for most purposes. Chemical precipitation by alum or other salts is likely to leave chemical residues in the water if treatment is not properly conducted. However, with alum treatment Edwards and Buswell (271) found that the alkalinity, iron, and Al_2O_3 are decreased. In general, this treatment would appear to improve the water. The alum treatment, however, undoubtedly removes much of normal life of the water. These methods should not be introduced into laboratories, without extended investigation.

Waters variously treated for domestic use are available in laboratories as few waters escape treatment. Before important researches are undertaken the water should be most carefully examined and fully tested. The installation of treatment plants at special laboratories will find abundant background in the numerous municipal plants (see Ellms (274)).

IV. APPARATUS FOR CONTROLLING GAS AND SALT CONTENT AND pH OF WATER

This control of the content of water has to be brought about by (a) reductions and (b) additions. It is rarely possible to simulate natural conditions by one process alone, and the production of a continuous flow of water of a definite content presents some, though not insuperable, difficulties.

The processes of reducing of gas and salt content consist commonly in heating or boiling, or in reducing the atmospheric pressure. These two processes have been employed in biological work. Precipitation by means of colloidal flocculents such as aluminum hydroxide are referred to above as chemical precipitation.

1. Chemical methods of reducing the content of water

These are numerous, but none of them are conducive to the growth or the normal combination of organisms. Oxygen may be removed by reducing agents. Carbon dioxide may be reduced by alkali. The nature of the reducing agent and its chemical effect must be fully inquired into (Greenfield and Buswell, 352).

The removal of certain salts may be accomplished by chemical means (271). Commonly, however, it is either an exchange of elements or a precipitate is formed which must be removed by filtering. While in a particular case such treatment may be useful, the investigator should familiarize himself with the chemical processes and residues and submit the water to biological tests (Gallaher and Buswell (320), McRoberts and Buswell (560)).

2. Content reduction by pressure reduction and boiling

Both these methods reduce all gases and precipitate salts, the solution of which is determined by the gases. Heating and boiling kill all the flora and fauna, but presumably pressure reduction leaves much of

it alive, at least for a time, though no actual observations are known to us. On the whole, pressure reduction is the more desirable method, if the water treated is suitable for the animals experimented upon before the treatment begins. However, when the water used is unsuitable boiling may be most desirable.

a. Apparatus for dissolved gas control in standing water. Johansen and Krogh (445) made a study of fish eggs at different oxygen

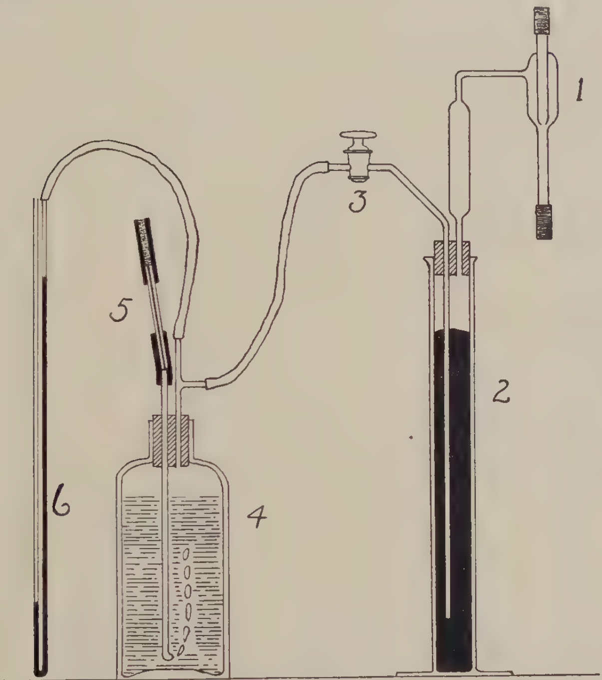

FIG. 210. Johansen and Krogh's oxygen control apparatus: *1*, aspirator pump; *2*, mercury valve; *3*, cock; *4*, experimental bottle; *5*, slow leak; *6*, manometer.

pressures. Their plan is shown in figure 210. Their apparatus consists in a filter pump which removes air faster than it can enter through a very small capillary tube. The action of the pump is reduced to a definite point by the mercury column.

With this type of apparatus, pressures were reduced to 225, 318, and 425 mm. Hg in different experiments. The air was introduced

and bubbled through the water at the reduced pressure. Small differences in the rate of development were brought about in plaice eggs by this method, amounting to 0.5 mm. reduction in the length of embryos in nineteen days after fertilization at 318 mm. as compared with 760 (7.1°C.).

b. Apparatus for controlling dissolved gases in running water. (1) By reduced pressure. The principle is essentially the same as in the

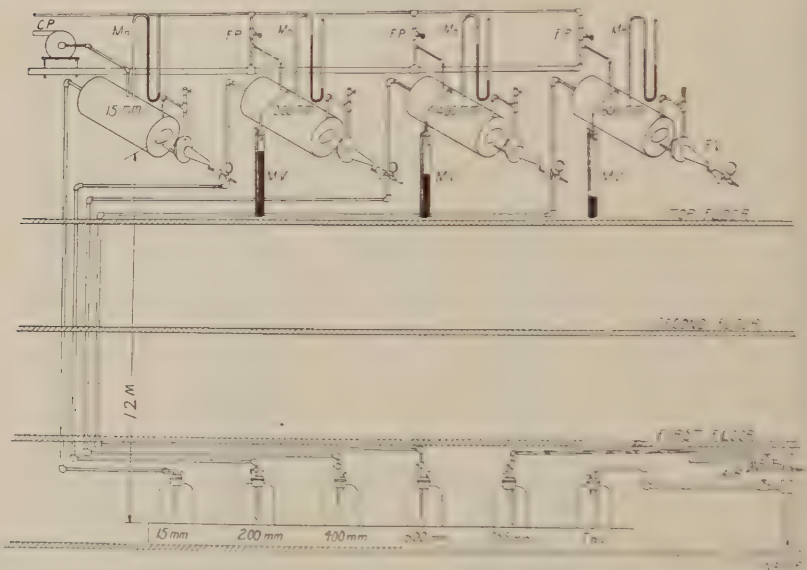

Fig. 211. Apparatus for controlling dissolved gases in running water. Four low pressure tanks are marked with pressure in mm. Hg. The air is exhausted by filter pumps or aspirators (*F. P.*) in three tanks. The fourth is exhausted by a centrifugal pump. Mercury valves (*M. V.*) hold the pressure constant, pressure may be read on the manometers (*Mn*). Water maintained at a constant level by water heater float valves (*F. V.*) The water is conducted to the second story below (more than 10 meters) and passes through the experimental bottle. The design provides for water aerated with compressed air and contact with the atmosphere in the bottle marked 755 mm. and for a bottle of direct tap water.

equipment for reducing atmospheric pressure and differs from the apparatus for standing water in that the air is introduced past the column of mercury. A ball float cock maintains the water at a definite level in the tanks and permits it to flow through at a definite rate.

The gas content is reduced to the pressure allowed by the mercury column. A manometer indicates this pressure.[1]

It is necessary to have the outlets 11 meters (35 feet) below the tanks to secure a flow pressure. It would be well, if it was procurable, to insert a plate with water tight connections with the sides and ends just below the lower side of the inflow pipe so that the incoming water will be spread out in a thin layer on entering and will not fall to the bottom, due to slightly lower temperature and greater salt content. A hand hole for cleaning the tanks and a means of emptying them entirely is required.

(2) Apparatus for controlling gases dissolved by boiling. The equipment at the University of Illinois consists of a large drain-table, shown in the lower part of figure 212 with the boilers on the floor above. The drain table is provided with double-decked towers 9 feet high, for supporting bottles, tanks, etc. Aside from possessing many advantages in the control of conditions where fluids and gases are added, the apparatus has great advantages in the control of oxygen content, as continuous flow is insured, and with aerating troughs of various lengths almost any amount of oxygen can be obtained in running water. An earlier apparatus used gas heat for boiling and could deliver not more than 100 cc. of oxygen-free water per minute, and this amount was not certain to be free from oxygen continuously. The new piece of apparatus delivers 1 liter of water per minute and could probably deliver a maximum of 4 or 5 liters per minute in a dissolved gas free condition but of pH 9.0.

High pressure steam at 60 to 80 pounds is used for boiling the water. The apparatus delivers it with the temperature brought down to that of the water supply. We may accordingly follow the course of the water supply from the supply pipe to the exit from the cooling coil. Water is introduced into the first boiler, *A*, from the supply pipe at the right of the upper group of apparatus. It is passed through a $1\frac{1}{2}$-inch strainer to an inclosed float cock, *FC*. This float cock, a stock article on the market, maintains water at a definite level in both tank *A* and tank *B*. Tank *A* is a water-heater containing a steam coil and vented by two large pipes connected with the flue. A large amount of steam and gas is given off from the water escape

[1] Carbon dioxide may be controlled in vessels by maintaining a constant pressure of the gas in the air above the water by means of a Leeds and Northrup apparatus described on page 242.

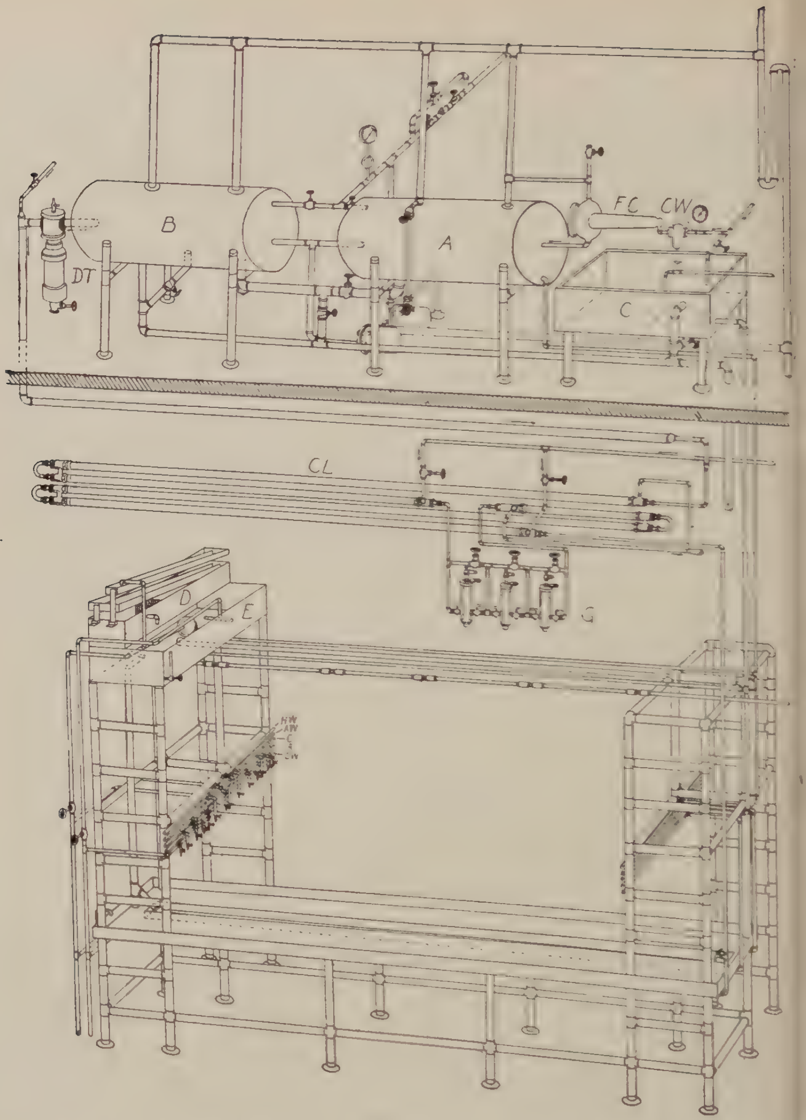

FIG. 212. Dissolved gas control apparatus installed at the University o Illinois Vivarium. The water is boiled first in tank A and later in tank B both of which are vented to the outside of the building. The water from condensation is discharged into the drain through a long loop trap, in the upper right hand corner. The water (CW) is supplied to the tanks by means of a float cock (FC) which maintains a constant level. The water is discharge through a dirt trap DT into a double pipe cooler (CL). Gases may be adde through the apparatus shown at G. The tank C is merely a tank to be fille with any desired kind of water. D is an aerating device supplying water t the tank E. The water table below is supplied with hot water (HW); aerate water (AW); water from tank C (C); air (A), and tap water ($C. W.$).

from this tank. Tank *A* is connected with tank *B* by a 2-inch pipe containing a valve which makes possible the draining of one tank without draining the other. The water being withdrawn from tank *B*, flows from *A* to *B* and is boiled for a long time in the latter, and is supplied with two vents in a large cover. The tank vents are connected directly with a 2-inch pipe which passes up a chimney; the condensation passes to a drain by way of a U-trap. The stream traps discharge into the drain (*D*) and are also vented into the chimney stock. The U-trap and vent are necessary to prevent steam escaping from the sewer opening into other rooms of the building. The water leaves tank *B* at the left through a dirt trap, and passes through the floor to the room below. The discharge line can be flushed with university water from *CW*. The steam used is high pressure—usually 90 pounds—but may be reduced to 25 or 30 pounds by a pressure-reducing valve. No steam or water can escape into the room.

After passing through the floor, the water goes through a cooler, *CL*, made from block-tin pipe (black iron return bends at the ends) placed inside $1\frac{1}{2}$-inch pipes connected with each other by cooler tees, the cooling water flowing into the cooler at the point where the boiled water leaves it. In the middle of the coil are three gas introducers *G*, which are modified air-purifiers formerly made by Bishop and Babcock, the gas being introduced into the chambers, through which the water flows, through blocks of basswood, thus dividing it into very small bubbles. Oxygen, carbon dioxide, and nitrogen have been introduced.

The water is delivered at the ends of a drain table. Tank *C* is used for securing water which is saturated with oxygen under atmospheric conditions in quantity sufficient to run through a number of bottles containing animals. Tank *D* is for aerating the university water-supply by running it down crimped inclines and through two chambers where the iron which is precipitated is removed. This water is stored in tank *E*. Two tanks like *D* and *E* are provided above tank *C*, with the controlling float-cock in *C*, so that water may be partially aerated and delivered to *C*, where compressed air forced into it renders it very alkaline and saturated with oxygen. The drain table is supplied with water from tanks *C* and *E* and from the university supply marked *CW*, and also with air (*A*).

(3) Apparatus for testing oxygen-free water (686). One of the

sources of error in the Winkler method for the determination of dissolved oxygen in water, especially where the oxygen content is low, is the diffusion of oxygen into the water before and during the introduction of the chemicals. Another source of error is the mixing of the manganous chloride with the potassium iodide-alkali solution at the surface of the water, the chemicals adhering to the pipettes introducing these reagents having washed off at the top of the bottle, where they react with the oxygen present. In recent work involving the oxygen-free water it was found especially desirable to eliminate these sources of error. This was accomplished by a special bottle which

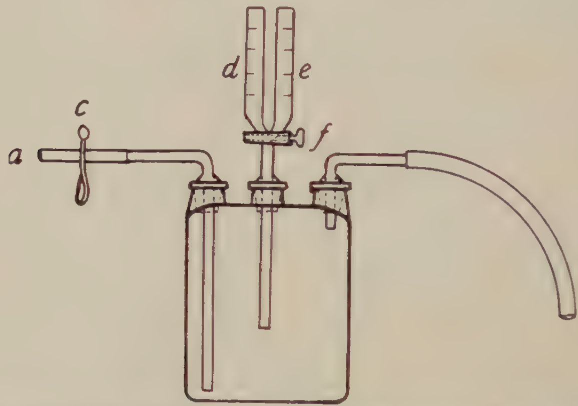

Fig. 213. Bottle for collecting samples and introducing Winkler reagents into water without contact with the air.

allows the collecting of samples and the introduction of the chemicals without exposing the samples to air during the operation.

The apparatus (shown in the accompanying figure 213) is composed of a bottle having an inlet, *a*, at bottom and an outlet, at top. When the bottle is filled the inlet is clamped off at c. The manganous solution is introduced through the burette *d* and the potassium iodide-alkali solution through the burette *e*. The burettes *d* and *e* are supplied with a two-way stop-cock at *f*. The displaced water is allowed to pass out at the outlet, which is kept open to equalize the pressure. The acid solution is introduced through the burette *d*, thus avoiding any action of a strong acid on the potassium iodide of the potassium iodide-alkali solution. A 200 cc. pipette is used to draw a sample for titration, thus avoiding agitation of sample in presence of

air. Correction for error due to the introduction of chemicals can be calculated from the per cent of collection used for titration with sodium thiosulphate, and the oxygen content of the water can be calculated directly. In lieu of the simple pipette for drawing off sample of water for titration, the device described by Shoub (838) may be substituted.

A modification of this bottle is also very useful for work with hydrogen sulphide, sulphur dioxide, carbon dioxide, and other gases when exclusion from the air is essential.

3. Distilled water

Distilled water is frequently needed in quantity in experimental work. That from the ordinary metal still is toxic to animals. For ordinary work one of the best sources in the writer's laboratory has been the condensation from the second dissolved-gas-free water boiler. The vent to this tank was obstructed and a part of the steam forced through a hard glass tube of 20-mm. opening and 1.6 meters long. Cold water was run through a piece of $1\frac{1}{2}$-inch iron pipe fitted with a $1\frac{1}{2}$ by $\frac{1}{4}$ inch tee at the inlet and a $1\frac{1}{2}$ by $\frac{3}{4}$ inch tee at the outlet end, the smaller opening serving to admit and the large one to drain off the cold water. The glass was held in place by large stoppers. About 40 liters of water could be secured per day with 60 pounds of steam and a good flow of cold water.

The water when collected was strongly acid from the presence of CO_2, which was removed by aerating with CO_2-free air. After aeration the water gave the following analysis:

Turbidity	0
Color	5
Odor	2V
	parts per million
Residue on evaporation, total solids	38.0 to 42.0
Alkalinity as calcium carbonate, methyl orange	26.0 to 36.0
Chlorides, as sodium chloride	0 to 0
Ammonium nitrogen	7.4 to 12.49
Albuminoid ammonia	0.06 to 0.102

This water was not rapidly fatal to fish. Two goldfish lived in it ninety-five and ninety-nine days and six blunt-nosed minnows survived eleven, twelve, thirteen, fifteen, thirty, and thirty-two days respectively. The water was changed every seven days. This

specially prepared water was used since it had been found that goldfish would live only from five to ten hours in ordinary distilled water condensed in metal (Powers, 1918).

V. CONTROL OF TEMPERATURE

1. General

Coolers for running water are often necessary in connection with brine systems. Due to the high specific heat of water, it is necessary to guard the refrigeration system against over-use of refrigeration by making the coils for cooling water of restricted capacity. Full efficiency will be attained far more readily than in the case of cooling air.

2. Methods of cooling

Where the use of running water would not be excessive, double pipe coolers adjacent to the aquaria to be supplied with water are desirable and most efficient for cooling 1–10 liters of water per minute from 2° to 10° where temperature permits. The same plan is effective with brine and with a sensitive pneumatic system which merely stops and starts the brine circulation. The chief danger here is in freezing the cooled water and bursting the pipes. At the University of Illinois, however, two such coils have been frozen several times without rupture. The brine pressure outside the water pipe gives a factor of safety.

a. Mixing two temperatures. A system in use at the University of Illinois consisted in mixing hot and cold water with an intermediate thermostat and three-way valves, the same type of mechanism used in mixing wet and dry air. The difference in temperature was great enough to give a rhythmic oscillation of temperature. It was very difficult to eliminate this and it was only possible by restricting the flow to a liter per minute and vigorously stirring the water in one-half of the aquarium while the animals were confined in another.

The general system of temperature control for the aquaria installed in the building proposed to mix refrigerated water and hot water to maintain all temperatures from 0° to 35°C. Thus with the ordinary supply at 18°C., a temperature of 18° would be maintained by mixing water at 0° and water at 35°. This resulted in overloading the refrigeration machines due to having one heating tank and one cooling tank to supply all the various temperatures. Such a system is highly

inefficient and ineffective so far as results are concerned. The operation of a series of aquaria of medium size took all the available refrigeration.

b. Dairy type coolers. The dairy products industry has developed economical apparatus for rapid and effective cooling. There are (*a*) simple cones through which cold water may be passed slowly while the fluid to be cooled is passed over the outside. Others are (*b*) coils through which water may be run while the fluid to be cooled flows over the outside (figs. 214, *A* & *B*). There are numerous (*c*)

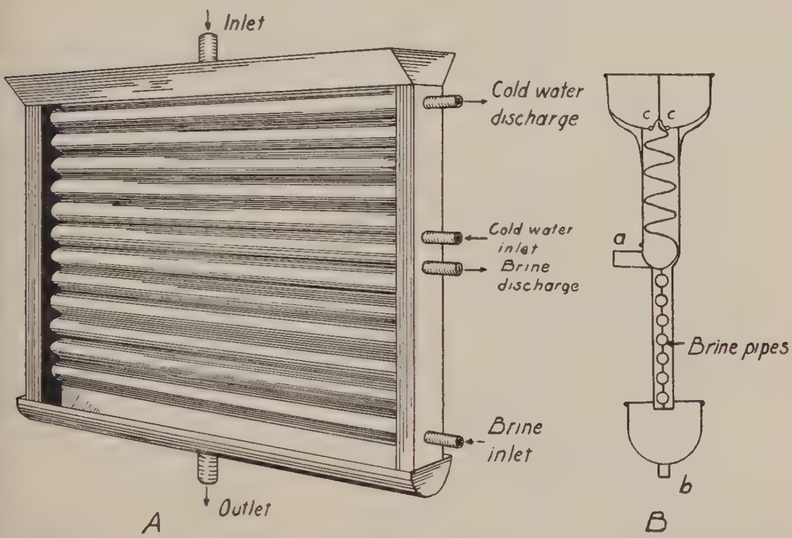

FIG. 214. Coolers. *A*, a cooler using both cold water and brine; *B*, is the cross-section of a regenerative cooler. The over-flow from a cold aquarium may be turned into the left side to cool fresh water coming in at the right.

double pipe coolers or heaters in which the inner pipe is filled with fluid to be cooled or warmed and the outer with the cooling medium. The open type (*b*), however, is advantageous for heating and cooling water as it permits an approach to saturation of the water with air at the temperature attained. Many of these are very effective, cooling a gallon or more per minute within 1°C. of the cooling medium.

Regenerative coolers are often of special value where the cooling medium must be used economically. The principle of the coils used is shown in figure 214, *A* and *B*. For example, when a regenerative

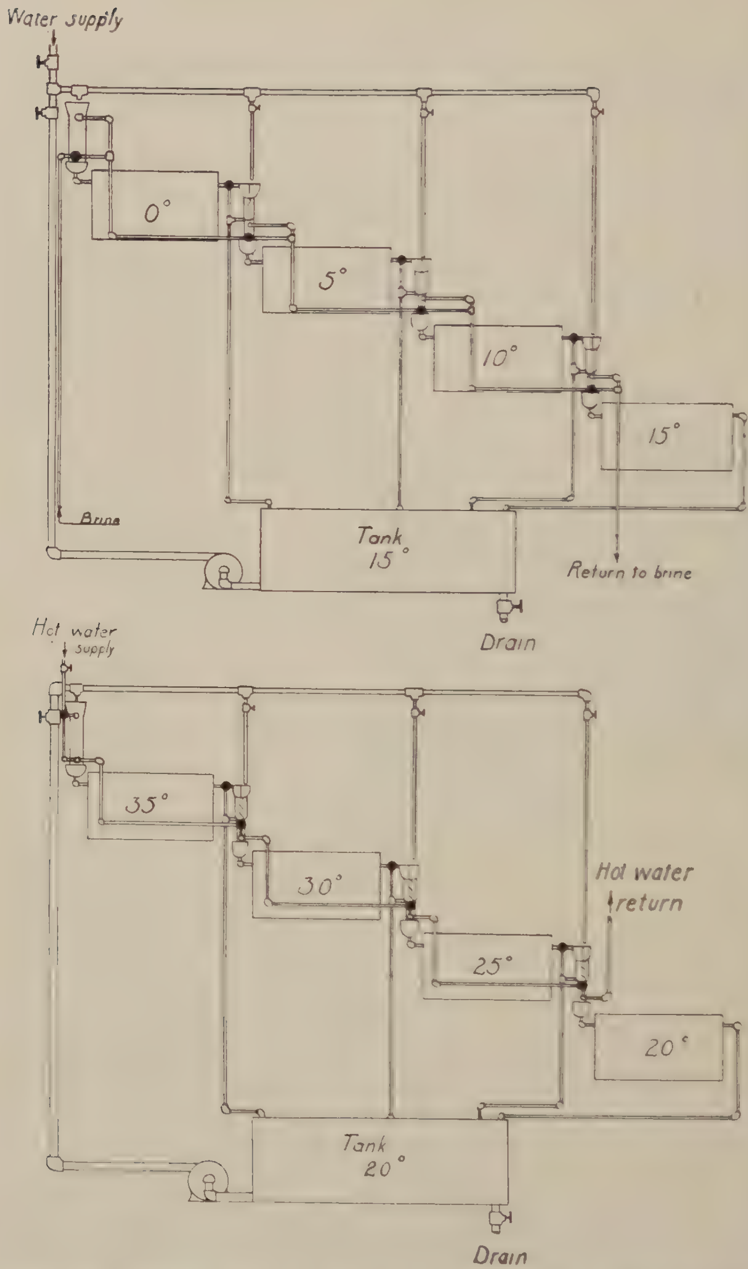

FIG. 215. Illustrating the use of regenerative coolers or heaters to maintain aquaria at several different temperatures.

coil like that shown in figure 214, *B*, is used, the cool milk on its way to the Pasteurizer is warmed by the milk returning from the Pasteurizer. Furthermore, the returning Pasteurized milk is cooled considerably at the same time. Another and important feature of the coils used is the fin extending downward from the center of the lower side of each pipe over which the fluid flows. These coolers have the advantage of also aerating the water. Figure 215 shows a design for aquaria using milk coolers, which may be purchased for about $40, with a capacity from 2 to 3 liters per minute cooled to within 1.2°C. of the

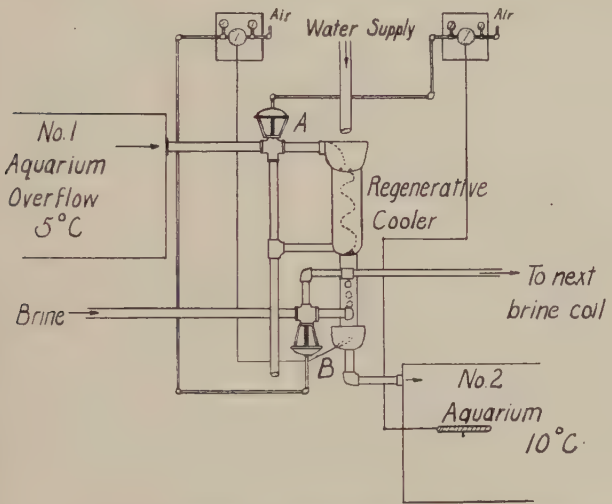

FIG. 216. Showing double intermediate thermostats and three way valves to maintain constant temperatures in aquaria. Three way valves are used and when the aquarium No. 2 is too cold the thermostat by passes a part of the overflow at (*A*). When the water leaving the coil is too warm the brine is turned on (*B*).

temperature of the cooling water. The so-called regenerative type is available but usually in large units. Double pipe coolers in which the milk is on the inside are available with removable return-bends permitting cleaning.

In a series of low-temperature aquaria, water is cooled for the first tank with a cooler of the type shown in figure 215. The drainage from the 0°C. tank flows through a coil of the type shown in figure 214, *B*, and partially cools the supply for the 5° tank, etc. The brine or cooling medium circulates through the entire series of coils, how-

ever. A similar series is shown for use with steam or hot water. This plan necessitates a stair step arrangement of the aquaria which makes it readily possible to run the water through a series. If the building is built for the purpose there is no difficulty with this arrangement. With aquaria holding water to a depth of 30 to 60 cm. series of no more than three aquaria may often be most economical to operate

Water may readily be run from one aquarium to the other, if desired. Such series of aquaria should be under thermostatic control. The Taylor Instrument Company's double duty thermostats as shown in figure 216 may be used.

The cooling or heating medium is always shut out of the coil so long as the overflow from the next aquarium is sufficient to produce the desired change of temperature. When it is not, the brine goes on and is regulated with the three way differential valve. Viscosity is so largely controlled by temperature that separate consideration is hardly necessary.

3. *Circulation control*

Within aquaria circulation is commonly brought about by small propellers operated by a small motor. The propellers are commonly covered with screen where current is desired.

The apparatus described on page 81 in connection with behavior may be made in any size; it gives a straight current of any velocity within ordinary natural limits. The flow may be regulated by regulating the volume of water and slope of the apparatus. For a gradient of current a series of three or four such troughs with the lower circle omitted and discharging across a suitable area with screen sides promises to give a gradient in current differing in speed from end to end. For example, there could be five troughs 5 cm. wide, discharging at 1, 5, 10, 15, 20 cm. per second across a screen-sided space 5 cm. wide. This has not been tested, but the two ends of such a space would differ as to current.

VI. THE HOUSING AND LIGHTING OF AQUARIA

The principles relative to lighting and arrangement of houses with reference to the sun are the same for aquatic appliances as for others. For plans for laboratories and glass-roofed houses, see page 388. Aquaria should be under ultraviolet transmitting glass, and to get best results the glasshouse should be conditioned to the point that it does

not get hotter than the outside air. The storage tank of recirculating systems should be in full light, and aeration should take the place of the usual darkness and filtration.

Aquaria may be made with sides and covers of any of the special glasses discussed. Lighting presents no new problems compared with climatic practice. Glasses must cover controlled aquaria in many if not most cases. The effect of the sun's ultraviolet on aquatic organisms is less well known than on terrestrial animals.

Controlled aquaria need to be kept free from dust and rain water and accordingly must be covered. For this reason, the placing of the aquaria in a building with roofs of ultraviolet transmitting glass is advisable. Aquaria with sides of various glass ray-filters should be employed.

The making and running of aquaria is so fully treated in texts and so well known in general that no further discussion is needed here. The keeping of animals alive, especially fishes in hatcheries, is well understood. Aquatic workers thus are partially prepared to undertake experiments in climate simulation. (See Richardson, 12.)

VII. CULTURE OF PLANKTON AND DIATOMS, ETC. (705)

As has been noted, many animals feed on particulate matter. We know no experiments in which this has been provided, but filtration certainly removes it. However, the cultivation of plankton diatoms and of other plankton organisms has been carried on with some success (24, 25, 433).

1. Culture of plankton diatoms (598)

a. Practical culture methods. These are described by Allen and Nelson (25) as follows:

1. Miquel's method. Attention was first directed to the culture of Plankton diatoms; and the methods, which had been elaborated by Miquel (25) for fresh-water diatoms and had been found by him to succeed with marine-bottom diatoms, were tried.

The essential features of Miquel's method, as applied to marine diatoms, are as follows:

Two solutions are prepared:

Solution A:

Magnesium sulphate	10.0 grams
Sodium chloride	10.0 grams
Sodium sulphate	5.0 grams

Ammonium nitrate	1.0 gram
Potassium nitrate	2.0 grams
Sodium nitrate	2.0 grams
Potassium bromide	0.2 gram
Potassium iodide	0.1 gram
Water	100.0 grams
Solution B:	
Sodium phosphate	4.0 grams
Calcium chloride (dry)	4.0 grams
Hydrochloric acid	2.0 cc.
Ferric chloride	2.0 cc.
Water	80.0 cc.

Forty drops of solution A and 10 to 20 drops of solution B are added to each 1000 cc. of sea-water, and the sea-water is sterilized by keeping it at 70°C. for about twenty minutes.

According to Miquel it is also necessary to add "organic nutritive material in the form of bran, straw, or filaments of weed such as Zostera. Macerations of these should be made up separately, some time before they are required for use, and should be carefully filtered and sterilized. Organic matter must, however, be used very sparingly, or else putrefaction will set in and the cultures will be irrevocably lost." As a matter of fact, we have found that such organic infusions are unnecessary, when dealing with plankton diatoms, and it has not been our practice to employ them (*cf.* however, [Allen's] p. 445).

Miquel (598) obtained cultures of single species of diatoms either by picking out individual diatoms and other organisms to some prepared water, and subdividing this into a number of tubes. If the subdivision has been carried out sufficiently some of the tubes may contain one kind of diatom only, from which fresh cultures can be made. In this way, by repeated subdivision, cultures can be obtained which, by inoculating fresh quantities of prepared water from time to time, may, with care, be maintained indefinitely. Such cultures, however, must practically always contain bacteria, and Miquel distinguishes them from bacteria-free cultures, which he terms "Cultures des Diatomees a l'etat de purete absolue." The latter he found very difficult to obtain, but, through repeated washing in sterile water, followed by fractional subdivision, he succeeded in getting some in which he could find no trace of bacteria by ordinary bacteriological methods (cf. Miquel 11, p. 155; cf. also Richter, 16–18 [see (25)]).

We propose to call any diatom culture, which can be carried on practically indefinitely by inoculating fresh supplies of prepared water, a "persistent" culture, the term "pure" culture being reserved for cultures which can be proved to contain not more than one organism. We are not satisfied that we have yet succeeded in obtaining cultures of the latter kind. For the most part our persistent cultures contain one species of diatom only, and are free from all organisms larger than small flagellates.

In our earlier experiments with plankton diatoms, we obtained persistent cultures, containing a single species of diatom, by both of the methods recom-

mended by Miquel. We, however, have rarely succeeded by picking out single diatoms or chains of diatoms, for although we have passed the selected diatom through several changes of sterilized sea-water, the resulting cultures, even when the diatoms have multiplied to some extent, have generally shown evidence of contamination by harmful organisms, and have soon died down. Only in one of the earliest experiments, and in one more recent, has complete success resulted. In the first case a small chain of six or eight frustules of *Skeletonema costatum*, picked out in April, 1905, gave rise to a culture which still persists (Nov., 1909). Subcultures can still be obtained even from the original flask inoculated in April, 1905. In the second case a chain of 8 or 9 cells of *Chaetoceras densum*, picked out from a Petri dish culture, has given a particularly good growth.

The method of dilution and subdivision has been more successful and persistent cultures of a number of species have been obtained in this way.

A more ready method of obtaining the cultures is, we have found, to add one or two drops of plankton to say, 250 cc. of a suitable sterile culture medium, and to pour this into shallow glass dishes (Petri dishes). The dishes should be placed in a position as free as possible from vibration, and where they can be easily examined with a lens *in situ*. The temperature should be kept as constant as possible and the dishes exposed to light of moderate intensity, direct sunlight being avoided. In the course of a few days, colonies of diatoms of different species will be seen at different spots on the bottom of the Petri dishes. These can be picked out with a fine pipette and transferred to flasks containing fresh culture medium. The colonies should be picked out from the Petri dishes at as early a stage as possible, because it left too long some one organism, a diatom or a flagellate, may have multiplied so rapidly that the whole of the water in the dish becomes infected with it. In this case persistent cultures of a single species would not be obtained. The above method is similar to one described by Miquel, excepting that he placed gelatinous silica at the bottom of the vessel. Some very successful persistent cultures were obtained from the following experiment, which will serve to illustrate the method:—A sample of plankton, from a very fine-mesh bolting-silk tow-net, was diluted down with sterile sea-water, until a single drop examined under a two-thirds-inch objective contained on an average ten organisms, chiefly diatoms of various species. Petri dishes (4 inches),containing 60 cc. each of Miquel sea-water, where then inoculated with various numbers of drops of the diluted plankton. The two dishes, to which two or three drops respectively were added, gave the best results; and from these persistent cultures of several species of diatoms were obtained. Hence we may conclude that the most advantageous number of single cells or short chains of cells to be added to a 4 inch Petri dish, containing 60 cc. culture medium, is about 20 to 30.

We have succeeded in obtaining the following species of Plankton diatoms in persistent cultures:—

Asterionella japonica, Cleve.
Biddulphia mobiliensis (Bail.), Grun.
Biddulphia regia (M. Schultze).
Chaetoceras densum, Cleve.
Chaetoceras decipiens, Cleve.
Chaetoceras constrictum, Gran.

Cocconeis scutellum, Ehr. var. *minutissima*, Grun.
Coscinodiscus excentricus, Ehr.
Coscinodiscus Granii, Gough.
Ditylium brightwellii (West), Grun.
Lauderia borealis, Gran.
Nitzschia closterium, W. Sm.
Nitzschia closterium, W. Sm., forma *minutissima*.
Nitzschia seriata, Cleve.
Rhizosolenia stolterfothii, H. Perag.
Skeletonema costatum (Grev.)
Streptotheca thamensis, Shrubs.
Thalassiosira decipiens, Grun.

It is hardly necessary to add that in dealing with these cultures, similar precautions to those used in bacteriological work must be taken, all vessels and instruments being carefully sterilized before they are brought into contact with the prepared sea-water. The cultures are best made in small, wide-mouthed flasks, which may be plugged with cotton wool, or simply covered with watch-glasses. The flasks should be kept at as uniform a temperature as possible (from 12°–17°C.) and should be exposed to strong daylight, direct sunlight being avoided. A flask should not be more than half filled with culture fluid, so that the surface exposed to the air may be large in proportion to the volume of fluid.

2. Crustacea (58, 215, 613, 969)

Whether the solutions used for algae are beneficial or detrimental to animals is not clear. Klugh's (1007) recent summary of literature and extensive experiments cover the effects of light, hydrogen ions and salt concentration upon Entomostraca as well as culture methods. The chief food of the Entomostraca in his experiments consisted of planktonic algae though some species made use of detritus. He found Moore's solution best for the growth of such aggregations.

The Crustacea commonly grown in cultures are the Entomostraca of the plankton type, especially Daphnia, and methods of rearing them are covered in the citations above. Such Crustacea are necessary for rearing fishes and other larger animals (1012).

3. Rotifers and Protozoa

Rotifers have been studied by Naumann (614). Peters (688) has made studies of the food substances necessary for the growth of Protozoa in cultures. Eddy (1008) studied succession in cultures for which materials were drawn from ponds and streams as well as cultures made from the usual materials.

APPENDIX

I. Records

A well-planned system of bookkeeping is essential in experimental work. The writer has used a system as follows:

Records of experimental work were made on ledger sheets, legal size, $8\frac{1}{2}$ by 14, printed with a special heading bearing the name of the project and calling for the name of the observer in the upper right hand corner; experiment number, date and species immediately below this; while at the right of the center were the words "Subject of Experiment;" below this, description of apparatus; and a line calling for notes on light, temperatures, together with previous history and condition of the stock. The lower 11 inches of this paper was ruled in quarter inch rulings, with 21 vertical rulings made $\frac{3}{8}$ inch apart, and leaving a square space of $\frac{1}{2}$ inch at each margin. Down the center of the page was a double blue ruling, which constituted one of the equidistant sets, and on each side of this three red rulings which constituted three of the equidistant sets. This type of paper was found to be particularly useful where a large number of individuals had to be checked daily as their numbers were put at the heads of the vertical columns and the dates in the left hand margins, the checkings in each square to show the condition of the individuals from day to day. The upper left hand corner of this paper was clear of printing or writing for the equivalent of a triangle with its sides 3 inches. This left a space in which no writing was ever placed, which made easy the fastening together of the sheets with various types of clips without interfering with the writing of the notes. These were gotten up for the current experiments and placed on legal size board clips which the investigator carried about with him as he observed the conditions of the experiments from day to day. The different chambers in which these experiments were performed were lettered, beginning with the large constant temperature rooms which were lettered A and B; then the variable units which were lettered C, D, E, F, G, H, and the small constant-temperature chambers, I, J, K, L, M, and N (see p. 120).

Then the smaller units inside the constant temperature rooms were numbered 1A, 2A, 3A, etc. With the maximum amount of experimental work going on, the entire alphabet was used in designating chambers and places in which animals were kept. For convenience of records and conversation with assistants and caretakers some such plan is necessary. When once adopted, these letters were allowed to stand in subsequent years for all the permanent pieces of the equipment.

In addition to the letters used to designate the various experimental chambers, the following were used with meanings as indicated:

For Humidity: D, Dry; M, medium moist; W, moist; WW, very moist.

For air movement and evaporation: H, high air velocity; I, intermediate air velocity; L, low air velocity.

For light: Dk, dark, L, light; LL., lighter.

For unit R (and ice-box): L, lower shelf; LL, lower left shelf; M, middle shelf; T, top shelf, etc.

O is out of doors; P, in the glass roofed house; NC, indicates no container, e.g., pupae in room atmosphere.

a, b, c, indicate different experiments under the same approximate conditions and from the same generation but started on different dates in the order indicated by the alphabet.

NV indicates that no air was forced through the container, hence not ventilated.

Thus 3ADa 1927 means unit A, small chamber 3, which is low humidity, and the first experiment in 1927.

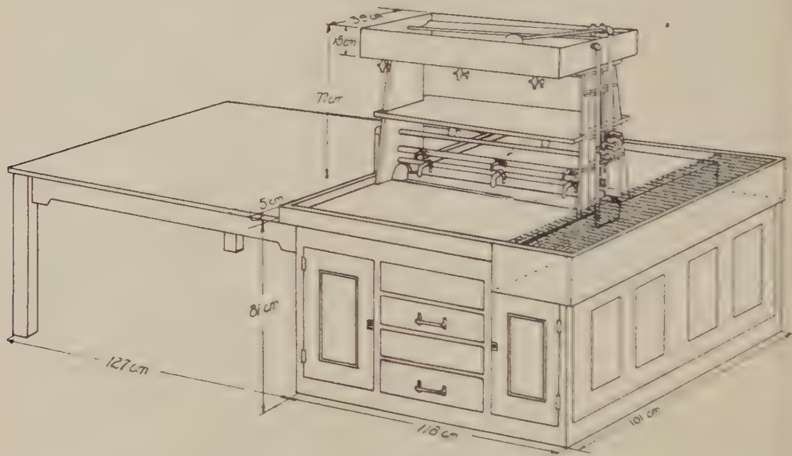

FIG. 217. A student table; for description see text.

The records of the codling moth work done for the Natural History Survey were kept on the special ruled paper already mentioned, the heading being properly filled out, and the numbers were inserted on the celluloid above the individual larvae and corresponding numbers at the heads of the long columns on the experimental sheet. The observer looked over the experiments morning and evening. A small check indicated that the larvae were still larvae; P was used to indicate that the larvae had pupated; E that they had emerged; D that they had died; M that they were missing; and K that they were accidentally killed, a single letter being inserted to indicate the condition at time of observation. It was very desirable ordinarily to indicate that the animal was actually observed and a record made of it by a check mark, as later on one might wonder if there was no record kept, or if something new had occurred whether he had actually looked at it or not. The check marks avoided this form of uncertainty in working over the results. In counting the days which

elapsed from the time of pupation to the time of emergency or any other period, clerks were first put to work ruling the sheets into days, where the observations were made twice a day, which was the case in all except the low temperatures. They were warned especially to look out for any irregularities of times when observations had been missed, as was sometimes necessary, particularly with the heavy program and in some of the lower temperatures where little progress was made, which were ordinarily looked over twice a day. These clerks drew

Fig. 218

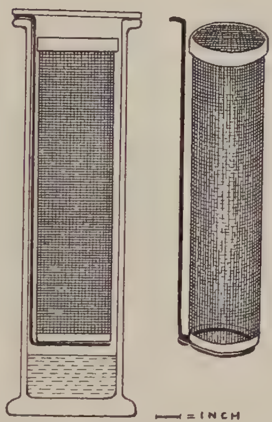

Fig. 219

Fig. 218. Screen-ended box, into which aquatic animals are placed and water allowed to run on to them from small cocks above. The water is about $\frac{1}{2}$ inch deep.

Fig. 219. An hydrometer jar with cage and wire to hold it up from the bottom in which there is about two inches of water. Land animals supplied with fresh plants every few days will live in these for months.

a horizontal red line across the paper, separating the days, then starting with the date of pupation, for example, they checked each corresponding reading; thus if the pupation occurred in the forenoon they checked each subsequent forenoon reading; if the afternoon, each subsequent afternoon reading. All were checked to the first, and at the same time the person counted the number of days from the time of pupation until the time of emergence, or whatever

other phenomenon was being observed, and the number of days which had elapsed was written at the bottom of the column or at the end of the record of the particular individual. This made it possible for any person to rapidly check the work of the clerk, who was found to have carried out this plan with a great deal of precision, having rarely made any errors.

II. Equipment for Keeping Animals Alive (215, 815)

Figure 217 shows a student work table to accommodate two students on each side. Two lockers and drawers hold the student equipment, which has been described in Chapter III, with other things used. Each table is supplied with hot water, cold water, electric outlets, and compressed air. Each has also a large water-storage tank with a small aerating incline, supplied with cocks along each side. This represents an earlier method of aerating. It is sufficient to prevent the development of gas bubble disease, but for deep-well water the more complete aerating device is desirable. The water cocks in the tank have the additional advantage of supplying water for experimental work under low pressure, which is very desirable.

For the keeping of stream animals alive between the date of collection and the time for experiments, figure 218, a long galvanized iron box, $25 \times 5\frac{1}{2} \times 5\frac{1}{2}$ inches ($62 \times 14 \times 14$ cm.), with screen ends, is provided. A small stream of water is allowed to flow into it directly from the taps in the bottom of aerating tank. Animals live here for weeks or months. To bring such animals in, a large-bottomed bucket with about an inch of water in the bottom is the best for small fishes and nearly all other animals.

Land animals may be swept from the vegetation or otherwise collected, but when brought to the laboratory they usually live for only a few hours. A wire cage suspended over water and loosely covered with a glass plate as shown in figure 219, provides conditions in which they will live for days. Such cages have been used in very large hydrometer jars, battery jars, etc. Animals collected from vegetation are supplied with suitable plants, and those from under logs or from soil are accompanied by decayed wood or soil from their habitats.

III. Estimated Costs of Materials and Equipment

Outfit No. 1 ($15.00). With a sink and running water available, simple experiments with small animals at two temperatures (e.g., 16° and 21°C.) in dry and moist air (approximately 30 and 90 per cent humidity) may be carried on by means of the following equipment at a cost of $15.00.

Twelve 2-quart fruit jars.
Twelve no. 13 rubber stoppers (2-hole).
Two 20-inch wash tubs.
One glass aspirator pump.
Two thermometers.
Rubber tubing and glass tubing.
Sulfuric acid, glass wool, charcoal, and solder.

All the jars are to be placed in water, half of them in one tub to maintain the lower temperature by running water, and the rest in the other tub with

standing water to equalize the fluctuations of the room temperature. The suction pump is to be connected with one jar having connections with the four jars in which the animals are kept, to which dry air is supplied from jars containing sulfuric acid and moist air from jars containing water. Air from the acid jars is passed through jars containing glass wool and charcoal, to remove any acid carried over, before passing into the jars containing the animals.

Outfit No. 2 ($100.00). By trebling all the items in *Outfit No. 1*, and by adding the following equipment, at a total expenditure of one hundred dollars, means may be provided for experiments at four constant temperatures (e.g., 12°, 16°, 21°, and 28°C.) with three humidities each (approximately 30, 60, and 90 per cent):

One electric water-bath heater.
Four maximum and minimum thermometers.
Cork, asbestos, felt, or other insulating material.

Outfit No. 3 ($300.00). The simplest kind of variable-temperature and variable-humidity experiments, for comparison with these under the constant conditions provided for in *Outfit No. 2*, will bring the total cost up to three hundred dollars through the addition of the following:

One Friez hygrothermograph.
One wire screen cage.
Another glass aspirator.

The cage and the hygrothermograph are to be out of doors. One of the jars is to be set on a south-facing window shelf, so that the animals in it will be subjected to a temperature averaging between five and ten degrees higher than those in the cage. This jar is to be ventilated (by means of the additional aspirator) with outdoor air the humidity of which is known from the hygrograph record, so that the humidity at the higher temperature in the jar can be obtained from tables.

Outfit No. 4 ($1200.00). Fair control of conditions over a somewhat wider range of temperature and humidity, with variations in rate of air movement, may be obtained if space is available in a glass-roofed house provided with 110-volt alternating current, by the addition of the following equipment, involving the expenditure of at least twelve hundred dollars:

One hydro-turbine air compressor (fig. 97).
One ¼ horse-power electric motor.
Incubators, three with water tops (fig. 177) and one with water-jacket sides.
Six spray heads, with strainers.
Three thermostats.
Three electric fans.
Three cages with glass sides (fig. 178).
Three soil and water thermographs.
Three hygrographs.
Three maximum and minimum thermometers.
Heat coils, atmometers, etc.

Outfit No. 5 ($2500.00). Somewhat more refined experiments, taking account also of the effects of light, may be provided for by adding the following equipment to the facilities listed in *Outfit No. 4*, on a budget of twenty-five hundred dollars:

Two additional constant-temperature cages for low temperatures.

Two small refrigerating machines.

One Carrier air-conditioning cabinet.

Photographic "daylight" lamps.

A small plant built on the principles discussed in Chapter XVI probably can be built for $300,000 or less.

IV. Sources of Equipment

A. Temperature Control and Measurement

1. Thermostats
   a. Electric
      - Central Scientific Company, 460 East Ohio Street, Chicago, Ill. (Dekhotinsky bimetallic and double disk)
      - Johnson Service Company, Milwaukee, Wis.
      - Industrial Controller Company, Milwaukee, Wis. (relays)

   b. Pneumatic
      - Taylor Instrument Company, Rochester, N. Y.
      - Johnson Service Company, Milwaukee, Wis.

   c. Program Thermostats
      - Taylor Instrument Company, Rochester, N. Y.
2. Coolers (chiefly Milk Coolers)
   - Cherry Burrell Corporation, Cedar Rapids, Iowa
   - Bessire and Company, Indianapolis, Ind.
   - Creamery Package Company, Chicago, Ill.
   - Crane Company, Chicago, Ill.
3. Refrigeration Machines
   - General Electric Refrigerator (small units)
   - Frigidaire Corporation, Dayton, Ohio (small units)
   - Carrier Engineering Corporation, Newark, N. J.
   - Audiffren Refrigerating Machine Company, 285 Madison Avenue, New York City
   - American Carbonic Machinery Company, Wisconsin Rapids, Wis.
   - Builders Iron Foundry, Providence, R. I. (Brine flow meters, venturi meters)
4. Automatic Valves for steam, brine, and water
   - Taylor Instrument Company, Rochester, N. Y.
   - Johnson Service Company, Milwaukee, Wis. (Pneumatic and solenoid valves)
5. Temperature Recorders (with one or two thermometers)
   - (See Friez, Green, Negretti and Zambra, and Jules Richard under weather instruments)
   - The Bristol Company, Waterbury, Conn.

The Foxboro Company, Foxboro, Mass.
Taylor Instrument Company, Rochester, N. Y. (With 1 to 16 insertion thermometers or thermocouples)
Leeds and Northrup Company, 4901 Stenton Avenue, Philadelphia, Pa.
Cambridge Scientific Instrument Co., Grand Central Terminal, New York. (Calendar recorder)

6. Precision Thermocouple Indicators
Leeds and Northrup Company, Philadelphia, Pa. (Potentiometers)
—Pyrolectric Instrument Company, Trenton, N. J. (Pyrovolter)

7. Chambers
Thermo Electric Instrument Company, Newark, N. J. (Freas incubators and water baths)
Central Scientific Co., 460 E. Ohio St., Chicago, Ill.
Dr. Chester I. Bliss, U. S. Bureau of Entomology, New Orleans, La. (Can supply blueprints of the Columbia University type of air circulating incubators)

B. Humidity, Evaporation, and Pressure

1. Humidity

a. Measurement
Chicago Apparatus Company, 1733 N. Ashland Boulevard, Chicago. (Dew point apparatus)
Leeds and Northrup Company, Philadelphia, Pa. (recorder)

b. Control
Carrier Engineering Corporation, Newark, N. J.

c. Humidostats
Johnson Service Company, Milwaukee, Wis. (Electric and pneumatic humidostats)
Taylor Instrument Companies, Rochester, N. Y.
American Blower Company, Detroit, Mich. (Hair humidostat)

2. Evaporation
B. E. Livingston, Johns Hopkins University, Baltimore, Md. (Livingston atmometers)
Bristol Company, Waterbury, Conn. (Liquid level recorders; may be used with open pan evaporation work)
Jules Richard, Paris. (Filter paper evaporation recorder)
C. G. Bates, University Farm, St. Paul, Minn. (Bates, or Forest Service, atmometer)

3. Pressure

a. Differential Draft Gauges
Lewis M. Ellison, 214 West Kinzie Street, Chicago, Ill.

b. Recording gauges (see under weather instruments)
Foxboro Company and Bristol Company

c. Control
Taylor Instrument Companies, Rochester, N. Y.
Mason Regulator Company, Boston, Mass. (Pressure regulating devices)

C. Weather Instruments
  Julien P. Friez & Sons, Baltimore, Md.
  Henry J. Green, Brooklyn, N. Y.
  Negretti and Zambra, 38 Holburn Viaduct, E. C., London
  Jules Richard, 25 Rue Mélingue, Paris

D. Light Measurement
  1. Thermopiles and bolometers
    Cambridge Scientific Instrument Company, Grand Central Terminal, New York. (Angstrom and Callender pyrheliometers—the latter is recording; also photo-electric cells)
    J. P. Foerst, University of Wisconsin, Madison, Wis.
  2. Photo-electric cells, selenium cells
    The Gaertner Scientific Corporation, 1201 Wrightwood Avenue, Chicago, Ill. (G and M cells)
    General Electric Company, Schenectady, N. Y. (Gas filled or vacuum cells)
    Case Research Laboratory, Auburn, N. Y. (Strontium vacuum cells)
    Electric Bean Grader Products Company, Ithaca, Mich. (Selenium cells—known to the writer only by advertisements)
  3. Illuminometers
    Leeds and Northrup Company, Philadelphia, Pa. (Macbeth illuminometer)
    Cambridge Scientific Instrument Company, Grand Central Terminal, New York
  4. Spectrometers, spectrographs, etc.
    Adam Hilger, Ltd., Camden Road, London, England
    Carl Zeiss, Inc., 485 Fifth Avenue, New York, N. Y. (Direct reading pocket spectroscope with scale)
    P. J. Kipp & Zonen, Delft, Holland. (Infra-red spectrograph)
  5. Quartz and glass (ray filters)
    Thermal Syndicate, Ltd., 58 Schenectady Avenue, N. Y. (Quartz and quartz-like glass)
    Corning Glass Works, Corning, N. Y. (All kinds of glass especially the noviols and ultra violet transmitting)
    American Optical Company, South Bridge, Mass.
    Carl Zeiss, New York. (All kinds of ray filters)
    Eastman Kodak Co., Binghamton, N. Y. (Gelatine ray filters, celluloid glass substitutes)
  6. Galvanometers—Unipivot and other portable instruments
    The Rawson Electrical Instrument Company, Cambridge, Mass. (Unipivot)
    Herman H. Sticht, 15 Park Row, New York City. (Unipivot)
    Cambridge Scientific Instrument Company, Inc., Grand Central Terminal, New York
    Kipp and Zonen, Delft, Holland. (Galvanometer deflection magnifier)
    Leeds and Northrup Company, Philadelphia, Pa. (Ship's galvanometers, portable galvanometer)

Artificial Lights
- The Photogenic Machine Company, Youngstown, Ohio. (White flame arc)
- The Butler Sanker Company, 321 Frankfort Ave., Cleveland, Ohio. (White flame arc.)
- General Electric Company, Schenectady, N. Y. (Flood light projectors)
- Edison Lamp Works (General Electric Company), Harrison, N. J.
- Cooper Hewitt Electric Company, Hoboken, N. J. (Mercury arc lamps)
- National Carbon Company, Cleveland, Ohio. (White flame carbons)

E. Water and Air Supplies
1. Centrifugal pumps and piping
   - Taber Pump Company, Buffalo, N. Y.
   - Chicago Pump Company, Chicago, Ill.
   - American Hard Rubber Company, 11 Mercer Street, New York, N. Y. (Centrifugal and reciprocating hard rubber pumps, pipe and fittings.)
   - Milwaukee Air Power Pump Company, Milwaukee, Wis. (Compressed air operated)
2. Air Compressors and Vacuum Pumps.
   - Nash Engineering Company, South Norwalk, Conn. (Hytor supplies washed air)
   - Johnson Service Company, Milwaukee, Wis. (Water operated)

F. Chemical Measurement
1. Hydrogen Ion Determination
   a. Colorimeters
      - Hynson, Westcott, and Dunning, Baltimore, Md.
      - The LaMotte Chemical Products Co., 13 W. Saratoga St., Baltimore, Md. (Includes one for small amounts of fluid)
   b. Electrometric Equipment
      - Leeds and Northrup Company, Philadelphia, Pa. (Precision, field and recording equipment)
      - Wm. Welch Scientific Company, 1516 Orleans St., Chicago, Ill. (Field outfit with quinhydrone cell)
2. Field Chemical Equipment
   - Burroughs Wellcome Company, E. 41st Street, New York, N. Y.

G. Sampling and Collecting Equipment
1. Marine and Fresh Water Equipment
   - D. Ballauf, 621 H Street, N. W., Washington, D. C. (Sounding machines, etc.)
   - Kelvin, Bottomley, and Baird, Ltd., 18 Cambridge Ave., Glasgow
   - Laboratorie Hydrographique, Prof. Martin Knudsen, Den Polyteecknicke Laereanstalt, Copenhagen. (Bottom samplers and marine equipment)
   - Northwest Instrument Co., Seattle, Washington. (Water bottles and other marine equipment)

2. Dredges and Bottom Samplers
   Coulter and McKenzie Machine Company, Bridgeport, Conn. (Oyster dredges)
   J. P. Foerst, University of Wisconsin, Madison, Wis. (Bottom samplers)
3. Small Mammal Traps
   Kny-Scheerer Corporation, 119-125 7th Avenue, New York, N. Y. (Hatt live trap)
   Abingdon Trap Company, Abingdon, Ill. ("It" trap—does not crush skull)

H. Delicate Glass Apparatus for Dissolved Gas Determination, etc.
1. Dissolved Oxygen
   Braun-Knecht-Heiman Co., San Francisco, Cal.
   (Thompson-Miller apparatus for micro-determination)
2. Oxygen Consumption, Carbondioxide Production, Air Moisture, etc.
   W. C. Flaig and Sons, 57 Hatton Gardens, London, E. C. 1.
   (Barcroft's apparatus for O_2 consumption)
   Paul Anders, 602 W. Nevada St., Urbana, Ill.
   (Osterhout's apparatus for CO_2 production)
   (Haldane's apparatus for O_2 consumption)
   (Rideal-Hanna acid hygrometer)
   E. H. Sargent and Co., 155 W. Superior St., Chicago, Ill.
   (Van Slyke apparatus)

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